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Bee Flies of the World
The Genera of the Family Bombyliidae

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A MONOGRAPH OF THE MONIMIACEAE (LAURALES) IN THE MALAGASY REGION (SOUTHWEST INDIAN OCEAN)^{1,2,3}

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ABSTRACT

A systematic, ecological, and evolutionary study of the Monimiaceae of the islands in the Malagasy floristic region, southwest Indian Ocean (Madagascar and the Mascarene and Comore archipelagos), is presented. The Malagasy Monimiaceae are here taken to comprise four genera and 55 species, all endemic: *Monimia* (3 spp., Mascarenes); *Decarydendron* (3 spp., Madagascar); *Ehippiandra* (6 spp., Madagascar); *Tambourissa* (43 spp., Madagascar, Mascarenes, Comores). Madagascar, a large, ancient continental island, is the regional center of diversity with three genera and 35 species. The smaller, younger volcanic islands harbor fewer taxa: Mauritius (2/11); Réunion (2/5); Anjouan (1/2); Grand Comore (1/1); Mayotte (1/1); Mohéli (1/1); Rodrigues (0). Synopses of the family's taxonomic history, biogeography, and distribution are given. The regional setting is defined and summaries of the geology, geomorphology, and climate of each island given. Distribution of species according to habitat is discussed for each island and ecological observations are presented. Vegetative and floral morphology and anatomy are described from both the literature and original observations. A synopsis of the palynology is given. Cytological investigations of ten species of *Tambourissa* revealed all to have $n = 19$. Results were inconclusive for *Monimia* but suggest it is polyploid with $n = \text{ca. } 44\text{--}48$. Field studies on floral biology of *Tambourissa* revealed that variations in floral morphology, color, and odor are responsible for several different pollination syndromes involving Coleoptera and Diptera. Breeding experiments demonstrated a strong tendency towards outcrossing via self-incompatibility in most monoecious species. Population density was related to pollinator systems in the three species studied.

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In the taxonomic treatment, keys to genera and species are provided. Synonymy, descriptions, distribution, habitat, discussions, vernacular names, economic uses, and herbarium specimens are given for each species. *Hedycaryopsis* Dang. is united with *Ehippiandra* Decne., thus necessitating the following new name and combinations: *E. domatiata* Lorence (basionym: *H. capuronii* Cav.); *E. madagascariensis* (Cav.) Lorence; *E. perrieri* (Cav.) Lorence. *Ehippiandra capuronii* Cav. is transferred to *Tambourissa* as *T. beanjadensis* Lorence. Finally, *Phanerogonocarpus* Cav. is united with *Tambourissa* Sonn. and the following new names are proposed: *T. alaticarpa* Lorence (basionym: *P. perrieri* Cav.); *T. longicarpa* Lorence (basionym: *P. capuronii* Cav.).

This monograph represents a systematic, ecological, and evolutionary study of the Old World Monimiaceae (Laurales) occurring in the Malagasy floristic region of the southwestern Indian Ocean, here taken to include the microcontinental island of Madagascar and its satellite islands, the Mascarene and Comore archipelagos (Figs. 1, 2). On many of these islands Monimiaceae constitute an important woody element of the wet and cloud forest formations.

Monimiaceae were chosen for study because they are a large and diverse but poorly known family belonging to the so-called "woody Ranales" that have played a key role in interpretation of the morphological and evolutionary patterns of primitive angiosperms. Extensive adaptive radiation into four genera and some 55 species, all endemic, in the islands of this region suggests that the Monimiaceae hold a unique position as a model for island evolution by a relict group of plants. Study of the family is all the more imperative in view of the threat posed by man's destructive activities in the region coupled with the relentless invasive competition from introduced plant species.

In spite of their importance as floristic components on many of these islands, the Monimiaceae have never been the subject of a detailed field study. Not only has there been a dearth of knowledge regarding their ecology and biology, but lack of field studies has also resulted in considerable taxonomic confusion because of the difficulty in matching androecious and gynoecious flowering material and of understanding morphologically variable species.

During the course of this work I was able to spend an entire year in the Malagasy region studying and collecting Monimiaceae in their native habitats in the following islands: Mauritius (where the majority of the work was carried out), Réunion, Madagascar, Mayotte, and Grande Comore. As a result, I have seen about half the species in the field and have accumulated a great deal of new ecological and biological information that is incorporated into this monograph.

TAXONOMIC HISTORY OF THE MONIMIACEAE

The Monimiaceae sensu lato are an old and diverse assemblage of about 30 genera and nearly 350 species widely distributed in the tropics and subtropics, especially in the southern hemisphere. The family has undergone a great deal of taxonomic flux because of the striking diversity of its members, which display various combinations of primitive and advanced characters.

Evolutionary advancement in floral morphology of the Monimiaceae is generally expressed in terms of reduction, both in size and number of parts; in rearrangement of their orientation from spiral to radial and finally to decussate; in closure of the female floral receptacle; and also in a transition from free stalked carpels to an inferior syncarpous gynoecium (Corner, 1976). Other advanced trends occur in wood anatomy, with simplification of the vessel members; in pollen; in leaf architecture; and in a progression from floral bisexuality to monoecy and finally dioecy. The Monimiaceae have a long and interesting taxonomic history dating back nearly two centuries.

De Jussieu first founded the family in 1809 (as Monimieae) based on three previously described genera: *Monimia* Thouars, *Atherosperma* Labill., and *Siparuna* Aubl. (as *Citrosma* Ruiz & Pav.). Tulasne subsequently monographed the family in 1855 (1855b), including seven additional genera and subdividing it into three tribes on the basis of characters of the fruiting receptacle. Baillon (1868–1870) circumscribed the family in a much broader sense to include the present day Calycanthaceae and Gomortegaceae, defining five series or tribes: Calycanthaeae, Hortoniaeae, Tambourisseae, Atherospermeae, and Gomortegaeae. Bentham and Hooker (1883) recognized only two tribes (Monimieae and Atherospermeae) based on features of the anthers and ovules, adding more genera but excluding the Calycanthaceae. This system was also followed by Pax (1891), who raised both tribes to the subfamilial level (Monimioideae and Ath-

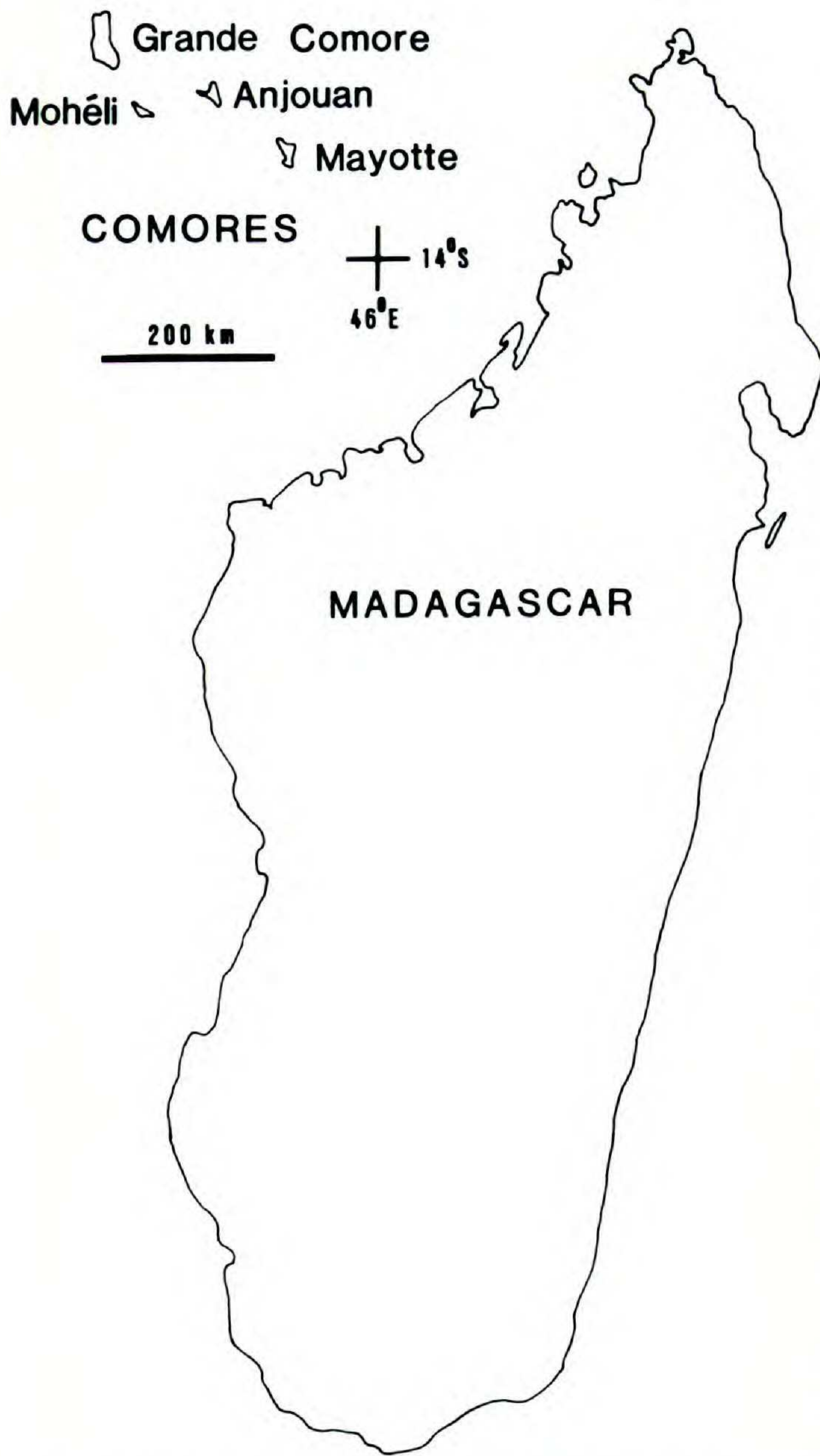


FIGURE 1. Regional map of study area, showing Madagascar and the Comore archipelago.

erospermoideae) and created six tribes for the species groups of Bentham and Hooker.

In their monograph of the family for "Das Pflanzenreich," Perkins and Gilg (1901) followed Pax, and Bentham and Hooker in recognizing two subfamilies but modified the tribes, creating an additional one under Monimioideae and merging two under Atherospermoideae. Perkins (1911) later updated the earlier revision using the same system. Hutchinson (1964) more or less followed Bentham and Hooker in dividing the Monimiaceae into two subfamilies, but recognized only four tribes.

As a result of its extreme diversity, many attempts have been made to dissolve the Monimiaceae sensu lato (Brown, 1814; Lindley, 1853; Pichon, 1948; Schodde, 1970; Smith, 1969). The

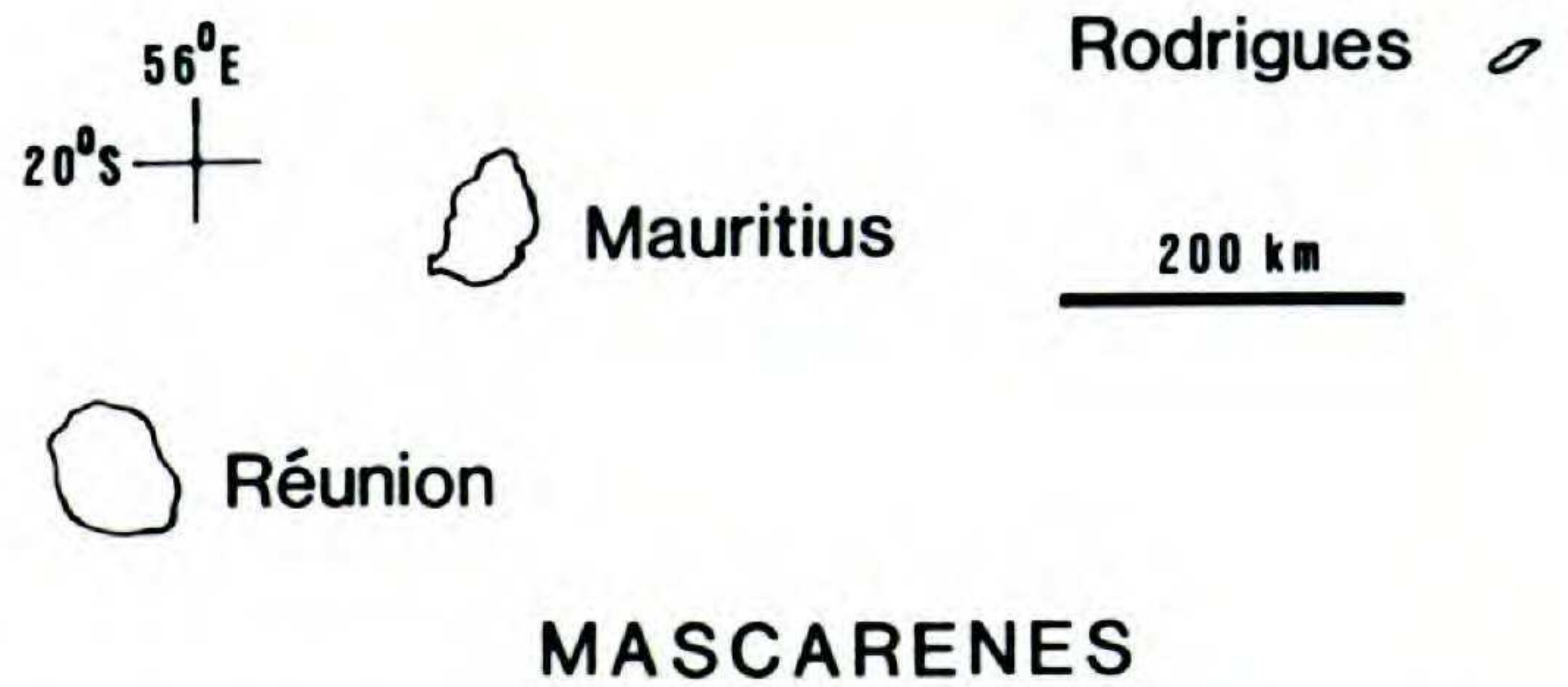


FIGURE 2. Regional map of study area, showing the Mascarene archipelago.

truly extraneous elements, however, notably *Amborella*, *Austrobaileya*, and Trimeniaceae, have been removed from the family by workers such as Pichon (1948) and particularly Money et al. (1950) in their important study of the morphology and relationships of the family. I agree with Thorne (1974) that the Monimiaceae sensu lato comprise a rather large and variable but coherent group with at least five major evolutionary lines derived from now extinct common ancestors. Recent morphological and anatomical studies by Sampson (1969a, 1969b), Endress (1980a, 1980b), as well as those by Money et al. (1950), support the rationality of treating these lines as subfamilies belonging to a single, diverse family rather than pursuing the alternative of splitting them into five separate families.

Hortonioideae, the smallest subfamily, contains three species in the unique genus *Hortonia* endemic to Sri Lanka (Ceylon). Its members possess an elaborate perianth with spirally arranged petaloid and sepeloid series, floral bisexuality, free stalked carpels borne on a discoid receptacle, basal staminal appendages, helical banded pollen, primitive wood anatomy, and the gametic chromosome number $n = 19$ (Money et al., 1950; Goldblatt, 1974; Endress, 1980a). Because it has retained the greatest assemblage of primitive characters, it has been considered to be most representative of the ancestral condition (Money et al., 1950), although recent studies by Endress (1980a) suggest it occupies a position intermediate between the Atherospermoideae and the Monimiaceae sensu stricto (i.e., Mollinedioideae plus Monimioideae of Thorne).

Members of the next subfamily, Atherospermoideae, are linked to the Hortonioideae by the similarly petaloid perianth and floral bisexuality of some members, and by their separate carpels borne on a shallowly concave receptacle. Advancements over the Hortonioideae include whorled arrangement of the parts and reduction

in their number, and a tendency towards floral unisexuality. The Atherospermoideae are characterized by having bisporangiate valvate stamens, erect, basal ovules (usually), a single nodal trace, advanced wood anatomy, and a basic chromosome number of $x = 22$. These plants also possess 1–2-colpate pollen and show a trend towards specialized comose, wind-dispersed carpels. The five genera and 12 species of Atherospermoideae have a strongly disjunct austral distribution ranging from Australasia to Chile, emphasizing the subfamily's great antiquity.

The Siparunoideae are also characterized by bisporangiate valvate stamens, erect basal ovules, a single nodal trace and a basic chromosome number of $x = 22$. These features are similar to those found in the Atherospermoideae, and the two groups probably represent lines of parallel evolution from a common ancestral stock (e.g., Schodde, 1970). The Siparunoideae, however, lack the basal staminal appendages, septate wood fibers, and hippocrepiform sclerids of the Atherospermoideae. Furthermore, advanced trends such as vessels with simple perforation plates, and closed, reduced floral receptacles with a velum replacing the perianth occur in the Siparunoideae in addition to other differences such as inaperturate, granulate pollen and bird-dispersed carpels. The subfamily comprises three genera: *Siparuna* with about 160 species in tropical America, *Glossocalyx* with three species in west tropical Africa, and *Bracteanthus* with a single species in Brazil. Thorne (1974) suggested that *Bracteanthus* may merit tribal or subfamilial status, and that Glossocalyxoideae be recognized as a subfamily (Thorne, 1983).

The largest subfamily, Mollinedioideae, contains about 18 genera and over 145 species (Thorne, 1983). Its members are characterized by having apetalous, unisexual flowers displaying various degrees of reduction and specialization, relatively primitive wood anatomy, and gametic chromosome numbers of $n = 18, 19, 22$, ca. 38, ca. 43, and 57 for various genera (Goldblatt, 1974).

Thorne (1974) united *Monimia* (3 species, Mascarene Islands) with *Peumus* (monotypic, Chile) as the sole members of the subfamily Monimioideae. Both genera have paired basal appendages on the stamens; large, spinose pollen, and comparatively advanced wood anatomy. This seems to be the most rational placement of these two genera in light of the available evidence.

Although recent subfamilial revisions of the Monimiaceae have been adequate (e.g., Thorne, 1974), all have neglected treatment at the tribal level. As Perkins' (1911, 1925), Perkins and Gilg's (1901), and Hutchinson's (1964) treatments of the subfamilies and tribes are outdated, a critical reassessment of the subfamilies of Monimiaceae at the tribal level is urgently needed.

GEOLOGICAL HISTORY AND REGIONAL SETTING

Beginning with a Jurassic Gondwana supercontinent, the formation of the Indian Ocean commenced as Africa (with India and Madagascar) rotated away from South America at the start of the Cretaceous (summarized by Fisher et al., 1967). At the same time the Antarctica-Australia mass began drifting southward, whereas the block comprising Africa-India-Madagascar remained intact until the mid-Cretaceous prior to about 90 Ma (Raven, 1979). At that time Madagascar occupied a position against the present Kenya-Somalia coast and was part of a Malagasy-Mascarene subcontinent joined to India via the now largely submerged Mascarene Plateau (Axelrod & Raven, 1978). Separation of this subcontinent from Africa occurred during the mid- to late Cretaceous at about 90 Ma (Raven, 1979). Probable separation of India from the Malagasy-Mascarene subcontinent occurred at the onset of its northward movement, about 70 Ma, which continued until it collided with the Asian landmass at about 45 Ma (Raven, 1979).

Formation of the present crescent-shaped Mascarene Plateau began with the separation of a portion of continental crust from Madagascar in the late Cretaceous or early Tertiary as Madagascar moved southward (Fisher et al., 1967; Kutina, 1975; Wild, 1975). This fragment, composed of Precambrian granites, included the present Seychelles archipelago and possibly the entire western flank of the Mascarene Plateau above the Saya de Malha bank (Fisher et al., 1967). Formation of the remaining portion of the Mascarene Plateau from the Saya de Malha southward to Mauritius was probably accomplished by late Cretaceous-early Tertiary submarine volcanic extrusions (Fisher et al., 1967).

The Rodrigues Ridge, from which Rodrigues Island emerges, is parallel to a fracture zone extending eastward across the Midoceanic ridge complex and was probably formed during the late Tertiary (Fisher et al., 1967). It is a volcanic

entity distinct from the Mascarene Plateau, separating the latter from Mauritius and Réunion (Fig. 2).

The Comore archipelago, situated between Madagascar and Africa (Fig. 1), is a product of successive Pliocene-Pleistocene volcanic eruptions (Esson et al., 1970). In contrast to Madagascar, which is a continental island, the Mascarenes and Comores are volcanic in origin and therefore strictly oceanic in nature.

GEOMORPHOLOGY AND CLIMATE

At present Madagascar is separated from the African mainland by the Mozambique channel, some 500 km wide at its narrowest point (Fig. 1). Situated midway between Africa and the northern part of Madagascar and separated on either side by depths of ca. 3,000 m are the four islands comprising the Comore archipelago: Mayotte, Anjouan, Mohéli, and Grande Comore. Stretching from ca. 800 to 1,600 km due east of Madagascar lies the Mascarene archipelago comprising the islands of Réunion, Mauritius, and Rodrigues. The Mascarenes are separated from the nearest landmass, Madagascar, by a stretch of ocean ca. 4,000–5,000 m deep.

MADAGASCAR

As the world's third largest island with an area of 590,000 km², Madagascar is truly continental in nature, consisting of a fragment of the original Gondwana landmass. Its large size, insular nature, and long isolation have made it an important refugium for many unique and relictual groups of plants and animals, including the lemurs. Its former connection to Africa and India once provided a route for Cretaceous dinosaurs and the rich angiosperm floras that appeared at that time (Raven & Axelrod, 1978).

Geologically, Madagascar is composed of four elements (Brenon, 1972). A much folded and outcropping metamorphic Precambrian basement in the form of a peneplain comprises the rugged central plateau which rises above 1,000 m (range 800–1,500 m) and also the highest mountains which are under 3,000 m (2,876 m at the Tsaratanana massif). This basement drops off abruptly along the great eastern escarpment down to a narrow coastal plain. Secondly, a slightly tilted Permo-Carboniferous continental sedimentary formation belonging to the Karroo system overlies the Precambrian basement and forms a band along the western third of the is-

land. Thirdly, basaltic volcanic formations belonging to upper Cretaceous eruptions form extensive flows in parts of the eastern and western regions and have given rise to certain mountain complexes in the north, center, and south of Madagascar. Finally, weathering and laterization of the Precambrian basement has resulted in a mantle of lateritic clays averaging 10–15 m thick overlying the bedrock. This is undergoing massive erosion accelerated by historic removal of much of the island's vegetation by man.

Madagascar's diverse geomorphology is the result of submersion and uplifting, pedogenesis and erosion, and scattered vulcanism during its long history. This edaphic diversity coupled with a variety of climatic types has resulted in the wide spectrum of habitats that exists in Madagascar.

Madagascar's position, considerable size (590,000 km²), and close juxtaposition of physical features such as lowland coastal plains gradually or steeply sloping to areas of medium altitude, and mountains exceeding 2,500 m elevation, are all responsible for its considerable climatic diversity (Donque, 1972).

First, its insular nature provides a maritime environment which is most prevalent in the eastern region. Here, warm oceanic currents moderate the temperature while moisture-laden trade winds and tropical cyclones impinging upon the east coast deposit heavy rains along the coast and eastern escarpment, permitting the development of dense, evergreen wet forest which forms a zone along the eastern third of Madagascar.

Second, Madagascar is sufficiently long (ca. 1,500 km) and wide (ca. 450 km average) to display many characteristics of a small continent. This continentality is reflected in a wide spectrum of temperature, atmospheric humidity, precipitation, and wind regimes. As a result of its longitudinal extension, the island possesses sub-equatorial regions in the north (at 12°S) where a monsoon climate and dry season modify the composition of the evergreen forest. In the south, it passes through the Tropic of Capricorn and extends into the subtropics at its southern extremity (25°30'S), giving rise to considerable thermal variation. On a latitudinal basis, both precipitation and temperature decrease considerably in the central uplands. Precipitation further decreases and temperature increases to the west and south as the Trade winds rapidly lose their remaining moisture and velocity due to the rain shadow effect. As a result, the vegetation

TABLE 1. Distribution of total Monimiaceae and *Tambourissa* species per island in the Malagasy region in relation to area, elevation, and age of island.

Island	Area (km ²)	Elevation (m)	Age (Ma)	Total Species Monimiaceae	Total Species <i>Tambourissa</i>
Madagascar	590,000	3,000	70† (as island)	35	26
Réunion	2,500	3,000	3.0	5	2
Mauritius	1,865	900	7.8	11	10
Grande Comore	1,148	2,400	0.01†	1	1
Anjouan	424	1,600	1.5	2	2
Mayotte	370	700	3.7	1	1
Mohéli	290	800	ca. 1.5	1	1
Rodrigues	110	400	1.5	0	0

becomes progressively more xeric in nature to the south and west, passing from sclerophyllous evergreen forest to semideciduous forest and finally thorn scrub and desert (Koechelin et al., 1974, give a detailed account of the vegetation).

Temperature, wind, and rainfall are further influenced by the island’s varied relief, giving rise to a spectrum of bioclimates varying in both temperature and precipitation. For example, some of the higher mountains extend into the cloud zone and harbor a montane cloud forest formation, above which occurs a low, ericoid scrub characteristic of the high montane zone.

This diversity of habitats and extreme ecological gradients in conjunction with Madagascar’s long isolation have resulted in high levels of floristic endemism: up to 48% of the genera and 95% of the species are endemic in certain regions (Koechelin et al., 1974; Leroy, 1978). It is therefore not surprising that Madagascar harbors the greatest constellation of Monimiaceous taxa in the region (three genera and ca. 35 species), Africa notwithstanding (Table 1).

MASCARENE ARCHIPELAGO

The three Mascarenes are volcanic oceanic islands that consist of the exposed summits of submarine mountain chains, i.e., Mauritius and Rodrigues, and an isolated volcano arising from an abyssal submarine plain, i.e., Réunion (Cadet, 1977).

All three islands experience a tropical insular climate moderated by the maritime effects of the warm ocean and the steady south-east Trade wind regime. Precipitation is most abundant during the warm and rainy austral summer season lasting from December to April, occurring as orographic rains resulting from adiabatic air expan-

sion, and also as heavy cyclonic rains. In addition to bringing rain, cyclones, with winds gusting up to 240–320 km/hr, are often destructive to the vegetation. On the average, direct hits by cyclones occur only once every 12 to 15 years. The relatively drier and cooler austral winter season lasts from May to November.

The mean annual precipitation ranges from 1,100 to 1,700 mm in Rodrigues (Lorence, 1976), and from 1,000 to 5,000 mm in Mauritius and Réunion (Lorence, 1978; Cadet, 1977). Mean annual temperatures in the Mascarenes are not extreme, ranging from 16 to 20°C in the uplands and from 21 to 25°C in the lowlands during the winter, and from 21 to 25°C in the uplands and 27 to 30°C in the lowlands during the summer.

Réunion, the largest (2,500 km²) and easternmost of the Mascarene Islands, is the summit of a volcanic cone rising some 3,000 m above sea level. Its active volcano, Piton de la Fournaise, still erupts frequently, emitting basaltic lavas similar to the Pleistocene flows in Mauritius (Fisher et al., 1967). Quaternary lavas from the Piton des Neiges flows have been dated at 2.1 Ma, although Fisher et al. (1967) suggest that submerged caldera flows may be older, possibly ca. 3 Ma (Cadet, 1977). Some subsidence appears to have taken place during the Quaternary, perhaps resulting in a small reduction of the island’s surface area. Coral reef development around Réunion is virtually absent.

In addition to its accentuated relief, Réunion’s 3,000 m altitude provides the greatest range of habitats of any of the Mascarenes, ranging from semideciduous dry forest and thicket in the western rain shadow, to lowland wet forest, montane cloud forest and high montane ericoid scrub and grassland. *Tambourissa*, with only two species here, is less abundant and much less diverse than

within the archipelago are a highly embayed coastline, development of the finest barrier reef and lagoon in the Indian Ocean, and occurrence of deep, red laterized soils (Guilcher et al., 1965).

Anjouan and Mohéli are both centrally located and represent the summits of extinct volcanos. Both are relatively old structures with eroded but still recognizable craters and cones. Anjouan is larger, attaining 1,595 m, and has an area of 424 km² with an accentuated relief and narrow but fringing coral reefs encompassing about two-thirds of the coastline. Its oldest lavas have been dated at 1.52 Ma (Hajash & Armstrong, 1972). Mohéli is the smallest of the Comores, rising to 790 m altitude with an area of only 290 km². Its relief is less rugged but its reefs are also wide and well developed, although its lavas have not been dated. Mayotte, Anjouan, and Mohéli are all volcanically extinct.

Grande Comore, largest (1,148 km²) and youngest of the four islands, has an active volcano whose summit attains 2,360 m, and is essentially a mass of scarcely eroded lava lacking permanent rivers and streams. The only dated lavas from Grande Comore are recent (0.01 Ma), although underlying flows are thought to be older (Hajash & Armstrong, 1972). Coral reef development around the island is sparse and embryonic, also reflecting its relative youth.

The Comores lie in the south-east Trade wind belt, although they are somewhat sheltered by Madagascar, and cyclones are rare. The drier and cooler winter season extends from May to October, the majority of the rain falling during the hot austral summer season from November to April (Manicacci, 1939). In 1935, the following annual rainfalls were recorded: Grande Comore, 4,254 mm; Anjouan, 1,411 mm; Mayotte, 869 mm (at Dzaoudzi, but probably double inland); Mohéli, 478 mm (Manicacci, 1939). Temperatures range from 25 to 35°C in the summer and from 18 to 25°C in the winter, depending on the elevation.

The Comores generally support evergreen moist or wet forest on their lower windward and mountainous slopes, and semideciduous dry forest in the low altitude regions of the rain shadow. Anjouan and Grande Comore have zones of cloud forest above 900 or 1,000 m, and this gives way to *Philippia* heath formation on the Karthala volcano massif on Grande Comore. Each island has but a single species of *Tambourissa*, except for Anjouan which has two (Table 1). Four of the five Comorean species of *Tambourissa* appear to

be closely related and may be derived from a common ancestor.

BIOGEOGRAPHY AND DISTRIBUTION

Biogeographically, it appears that direct migration of the Monimiaceae between Africa and South America occurred by the Eocene, after which widespread extinction took place in Africa (Raven & Axelrod, 1974; Axelrod & Raven, 1978). Fossils that have been considered Monimiaceous are known from the late Cretaceous (ca. 70–80 Ma) in Europe, Africa, and Argentina. In contrast to the widespread floral and faunal impoverishment that took place in continental tropical Africa (Richards, 1973, 1979), the Malagasy region provided an important refuge for many elements of the area's biota; for example, the lemurs in Madagascar and the Comores, and the now extinct flightless birds such as the dodo and solitaire in the Mascarenes (Carlquist, 1965).

The Monimiaceae may be thought of as botanical counterparts of the lemurs and are represented by four genera and about 55 species in the Malagasy region, all endemic. The isolation and habitat diversity offered by islands are well known to be conducive to rapid adaptive radiation (e.g., Carlquist, 1965, 1974), which is exemplified by the Malagasy area Monimiaceae. In marked contrast, only two genera of Monimiaceae have persisted in continental Africa—i.e., *Glossocalyx* and *Xymalos*—comprising a total of four species. This is primarily because the Monimiaceae attain their greatest diversity in premontane wet and montane cloud forest formations, habitats that are abundant in the Malagasy region but poorly represented in Africa. Furthermore, most cannot tolerate the ecologically significant dry periods that are characteristic of even the wet forest in Africa (Richards, 1973), although their absence from the cloud forests of the east African mountains is puzzling. Perhaps these forests were greatly reduced in extent during the dry periods of the Pleistocene, and Monimiaceae were unable to recolonize them from their more equable refuge areas on Madagascar and the Mascarenes.

Madagascar harbors three closely allied genera of trees and shrubs belonging to the subfamily Mollinedioideae. Of these, *Ehippiandra* (6 spp.) and *Decarydendron* (3 spp.), are endemic. Their inability to spread to the other islands may be a reflection of their poor dispersibility or seed viability. Alternatively, suitable habitats may be

lacking on the satellite islands. This does not appear to be the case, however, because relatively large and elevated islands such as Réunion and Mauritius offer many of the same habitats as Madagascar (Table 1).

Tambourissa, however, has reached six of the seven satellite islands where it has become established and undergone successful adaptive radiation (Table 1). Reports that *Tambourissa* occurs in Java (e.g., Cavaco, 1965) appear to be erroneous (see discussion under *T. ficus*), and the genus appears to be restricted to the Malagasy floristic region. Possible reasons for its success most likely include its bright red-orange drupes, which are ostensibly more attractive to birds (those of *Ehippiandra* ripen black) resulting in greater dispersibility, a greater seed viability (drupes of *Tambourissa* may take two or three months to germinate; D. Lorence, pers. observ.), and enhanced ability to compete and evolve rapidly. In any case, *Tambourissa* provides an excellent model for island evolution in a family of primitive angiosperms.

Monimia (Monimioideae) consists of three closely related species endemic to the Mascarene Islands of Mauritius and Réunion. Its absence from Madagascar is puzzling in view of its bird-dispersed carpels. *Peumus* in Chile appears to be its closest relative, although it also shares a number of features with *Palmeria* from Oceania (see discussion under *Monimia*).

HABITAT AND ECOLOGY

The majority of ecological and floristic studies or surveys conducted for the islands of the Malagasy region demonstrate or at least mention the importance of the Monimiaceae as woody elements of the vegetation (Vaughan & Wiehe, 1937, 1941; Humbert, 1965; Legris, 1969; Koechlin, 1972; Koechlin et al., 1974; Cadet, 1977). In addition, data from specimens provide much information.

MADAGASCAR

Although I am unaware of any specific ecological studies for Madagascar involving Monimiaceae, the broad vegetational surveys of Humbert (1965) and Koechlin et al. (1974) coupled with data from specimens which I have examined and those cited by Cavaco (1959) have enabled the habitat and distribution of most species to be established. A significant number of taxa, however, are known from only one or

several collections, possibly a result of undercollecting, which may therefore inaccurately portray their actual distributions. Of the Imperfectly Known *Tambourissa* species, only numbers 40 (*T. sp. A*) and 42 (*T. sp. C*), are included in this discussion, because collection localities for the others are either too vague or were not located.

Work done by Humbert (1965) and Koechlin et al. (1974) indicates that in Madagascar species of *Tambourissa*, along with *Weinmannia* (Cunoniaceae), are among the most frequent and characteristic components of the canopy in the montane wet/cloud forest zone. *Tambourissa* attains its greatest diversity here, with at least 14 of the island's 26 species occurring in this zone (Table 2) which forms a belt along the eastern part of the island from ca. 800 m and extends upward to the mountains of the central plateau to between 1,300 and 1,800 m. Annual precipitation here ranges from ca. 1,000 to 2,000 mm, with a short dry season.

In addition to *Tambourissa*, two endemic Madagascan genera also occur in this zone, *Decarydendron* (2 spp.) and *Ehippiandra* (3 spp.), bringing the total number of Monimiaceae to 19 (Table 2). The *Tambourissa*/*Weinmannia* zone is clearly Madagascar's richest habitat in terms of Monimiaceae species and genera.

In the east, this zone is subtended by a lowland wet forest of Myristicaceae and *Anthostema* (Euphorbiaceae) receiving an annual precipitation of ca. 1,500–3,500 mm and having no significant dry season. In addition to sharing about three species with the former zone, including *Ehippiandra madagascariensis* and two species of *Tambourissa*, this zone possesses a number of its own species, most notably *Decarydendron lamii* and five species of *Tambourissa*: *T. alaticarpa*, *T. castri-delphinii*, *T. decaryana*, *T. longicarpa*, and *T. sp. C*. Besides *T. castri-delphinii*, the wide-ranging *T. purpurea* and *T. religiosa* are the only Monimiaceae known to inhabit the coastal forests on sand dunes.

The lowland wet forest also extends to the small Sambirano region in the northwest, including Nosy Be Island, where it is further characterized by the presence of many Chlaenaceae, an endemic family. In addition to harboring such wide-ranging species as *Ehippiandra madagascariensis* and *Tambourissa purpurea*, the Sambirano area has two endemics: *T. nitida* and *T. nosybensis*.

At altitudes from ca. 1,800 to 2,000 m in the cloud zone on the mountains of the central re-

TABLE 2. Distribution of Monimiaceae according to habitat in Madagascar.

1. Lowland wet forest zone of Myristicaceae and <i>Anthostema</i> (ca. 0–800 m), including littoral forest and Sambirano region. <i>Decarydendron lamii</i> <i>Ehippiandra madagascariensis</i> <i>Tambourissa alaticarpa</i> <i>T. castri-delphinii</i> <i>T. decaryana</i> <i>T. longicarpa</i> <i>T. nitida</i> <i>T. nosybensis</i> <i>T. perrieri</i> <i>T. purpurea</i> <i>T. religiosa</i> <i>T. sp. C</i> (no. 42)
2. Medium altitude wet/cloud forest zone of <i>Tambourissa</i> and <i>Weinmannia</i> [ca. 800–1,300(–1,800) m]. <i>Decarydendron helenae</i> <i>D. perrieri</i> <i>Ehippiandra domatiata</i> <i>E. madagascariensis</i> <i>E. microphylla</i> <i>Tambourissa beanjadensis</i> <i>T. capuronii</i> <i>T. floricosata</i> <i>T. gracilis</i> <i>T. hildebrandtii</i> <i>T. humbertii</i> <i>T. madagascariensis</i> <i>T. perrieri</i> <i>T. purpurea</i> <i>T. religiosa</i> <i>T. thouvenotii</i> <i>T. trichophylla</i> <i>T. uapacifolia</i> <i>T. sp. A</i> (no. 40)
3. Sclerophyllous montane lichen forest zone (central mountains, 1,300–2,000 m). <i>Ehippiandra myrtoidea</i> <i>E. perrieri</i> <i>E. tsaratanensis</i> <i>Tambourissa gracilis</i> <i>T. parvifolia</i>
4. High montane <i>Philippia</i> ericoid heath formation (central mountains, above ca. 2,000 m). <i>Ehippiandra microphylla</i> <i>E. perrieri</i> <i>Tambourissa parvifolia</i>
5. Sclerophyllous moist forest zone of <i>Uapaca bojeri</i> and Chlaenaceae (western slopes of central domain, up to ca. 800–900 m). <i>Tambourissa hildebrandtii</i> <i>T. purpurea</i>

TABLE 2. Continued.

6. Semideciduous dry forest zone of western domain (below ca. 700–800 m). <i>Tambourissa bathiei</i> (probably riverine) <i>T. perrieri</i> (probably riverine)

gion, the *Tambourissa*/*Weinmannia* belt is replaced by a dense sclerophyllous forest with an abundance of epiphytic lichens. Perhaps because of the lower temperatures, the Monimiaceae drop out rapidly here (Table 2). *Ehippiandra microphylla* and *Tambourissa gracilis* are virtually the only species shared with the zone below. The only species characteristic of this zone and, to a lesser extent, of the high montane ericoid thicket superseding it beyond the cloud zone at above ca. 2,000 m are *Ehippiandra myrtoidea*, *E. perrieri*, *E. tsaratanensis*, and *Tambourissa parvifolia*.

The western slopes of the central plateau at and below ca. 800–900 m are characterized by a hotter, drier climate with more extreme temperatures. This area supports sclerophyllous forest of *Uapaca bojeri* (Euphorbiaceae) and Chlaenaceae, with only *Tambourissa hildebrandtii* and *T. purpurea*, two of the most widespread species, able to persist here.

In the dry western regions that extend to the coast, the sclerophyllous forest is gradually replaced by a semideciduous dry forest of *Dalbergia*, *Commiphora*, and *Hildegardia*. The only Monimiaceae found here are *Tambourissa bathiei* and *T. perrieri*, which apparently occur in riverine forests.

It should be emphasized that the vegetation of Madagascar, like most of the other islands, has undergone and continues to undergo severe degradation and destruction under the influence of man (Rauh, 1979). Because of its size, however, remnants of most and even fairly extensive areas of some vegetation types still remain (Rakotozafy, pers. comm.), but the need for their conservation is essential.

MASCARENE ISLANDS

On the average larger and older than the Comores, the Mascarene Islands also harbor more genera (two) and species (15) of Monimiaceae despite their greater isolation. In addition, the Mascarenes have been comparatively well stud-

ied floristically (Baker, 1877; Balfour, 1879; Cordemoy, 1895; "Flore des Mascareignes," in progress) and ecologically (Vaughan & Wiehe, 1937, 1939, 1941; Wiehe, 1949; Rivals, 1952; Cadet, 1977), thus permitting a more definitive assessment of the family's status there.

RÉUNION

Réunion is analogous to Grande Comore in being the only volcanically active member of its archipelago but is larger and older, supporting two genera and five species of Monimiaceae in contrast to the latter's unique species. Cadet's (1977) comprehensive study of the island's vegetation emphasizes the importance of the family as woody components of the flora. Although harboring the greatest expanse of indigenous forest of the three Mascarenes, many areas of Réunion are undergoing a dramatic invasion by vigorous exotic species such as *Psidium*, *Rubus*, and *Furcraea*, similar to that occurring in the other two islands.

Much of Réunion's lowland forest has disappeared, particularly in the dry western sector. Fairly extensive areas of lowland wet forest ("forêt mégatherme hygrophile" sensu Cadet, 1977) still remain above ca. 300 m, however, on the southern slopes of the active volcano, Piton de la Fournaise (at Mare Longue, Brûlé de Baril and other areas). Here a lush wet forest dominated by Sapotaceae (*Labourdonnaisia*, *Mimusops*, and *Sideroxylon*) has become established on the mosaic of lava flows where the rainfall averages 4,000–5,000 mm per year. *Tambourissa elliptica* subsp. *micrantha* appears here at ca. 300 m as a local, occasional to common component of the middle and upper strata and ranges to the mid or rarely upper limits of the wet forest zone (ca. 800–1,000 m) where it is generally replaced by *T. elliptica* subsp. *elliptica*. The latter is characteristically a smaller understory tree or treelet of occasional to common occurrence in both the wet forest zone below 1,100 m and the cloud forest zones (ca. 1,100–2,000 m) (Fig. 31).

The only other species to occur in the lowland wet forest zone of Réunion is *Monimia ovalifolia*, which appears at ca. 500 m and extends to ca. 1,700 m in the cloud forest zone. It typically forms local populations on sheltered slopes and in valleys and may become a canopy tree.

The lower limits of the cloud belt lie at ca. 800–1,100 m and mark the transition from wet to cloud forest ("forêt mésotherme hygrophile"

of Cadet), a zone characterized by lower temperatures and relatively constant high humidity. It is in the cloud forests of Réunion that *Monimia* attains its greatest abundance and diversity. The climax is considered to be the *Monimia/Dombeya* association ("Bois de couleurs") although *Acacia heterophylla* Willd. is dominant in some areas (Cadet, 1977).

Of the three *Monimia* species occurring in this zone, *M. rotundifolia* is by far the most abundant and widespread, codominant in many areas with species of *Dombeya* (Sterculiaceae) and other genera, e.g., at Col de Bellevue and Bébou forest (Fig. 22). Mature individuals 8–16 m high with dense, spreading crowns are often major components of the mid stratum and canopy. It occurs less frequently in the *Acacia/Nastus* forest and occasionally in *Philippia* heath up to ca. 2,000 m, with its lower limit extending down to ca. 1,000–1,100 m at the interface with lower altitude wet forest.

Monimia amplexicaulis is more restricted in distribution than *M. rotundifolia* and is generally confined to the mid and upper limits of the cloud forest, occasionally with *Acacia*. It characteristically forms discrete populations on the sheltered, leeward escarpments of the "cirques" or ancient volcanic calderas and is known primarily from the following localities where it usually replaces *M. rotundifolia*: Hauts du Tévelave, Plaine des Cafres, and Cirque de Cilaos (Fig. 22). An example of ecological differentiation between the two species was studied at Hauts du Tévelave, where *Monimia amplexicaulis* begins to replace *M. rotundifolia*, which occurs alone below ca. 1,700 m. Here, both species occur sympatrically at ca. 1,700 m along the Domanial line (Ligne Dominicale); neither intermediates nor hybrids were observed among dozens of individuals examined. The two species are easily recognized in the field and appear to maintain their integrity by flowering at different times.

Monimia ovalifolia is an occasional tree up to ca. 1,700 m altitude but is rarely abundant. It occurs sympatrically with *M. rotundifolia* in many localities, e.g., at Bébou forest where both species remain distinct and have different flowering times (Fig. 22).

Only two species of *Tambourissa* occur in the cloud zone: *T. crassa* and the macrophyllous upland form of *T. elliptica* subsp. *elliptica*. *Tambourissa crassa* is a light-demanding small tree which occupies the upper stratum of low forest or occurs in relatively open mixed heath at 1,200–

TABLE 3. Occurrence of Monimiaceae species according to habitat in Mauritius: indigenous plant communities.

	<i>Philippia</i>	<i>Sideroxylon</i>		High Forest:		Cloud	Semide-
	Heath:	Wet Forest:				Forest:	ciduous
	Pétrin;	Pieter	Bel	Macabé;	Brise	Mt.	Dry Forest:
	660 m,	Both;	Ombre;	660 m,	Fer;	Cocotte;	Yemen;
	pptn.	550 m,	300 m,	pptn.	600 m,	760 m,	200 m,
	4,000 mm	pptn.	pptn.	3,200 mm	pptn.	pptn.	pptn.
		2,400 mm	2,400 mm		2,400 mm	5,000 mm	1,600 mm
<i>Monimia ovalifolia</i>						X	
<i>Tambourissa amplifolia</i>			X	X			
<i>T. cocottensis</i>						X	
<i>T. cordifolia</i>	X						
<i>T. ficus</i>		X		X	X	X	
<i>T. pedicellata</i>		X		X			
<i>T. peltata</i>	X	X	X	X	X	X	
<i>T. quadrifida</i>							X
<i>T. sieberi</i>				X		X	
<i>T. tau</i>	X		X	X		X	
<i>T. tetragona</i>						X	

2,000 m. *Tambourissa elliptica* subsp. *elliptica* is a slender, sciaphilous understory forest treelet (1,100–2,000 m). Both species are occasional woody elements of the cloud forest (Fig. 31).

On the tops of exposed crests and at altitudes above ca. 1,700–2,000 m the cloud forest gives way to a low ericoid heath formation dominated by *Philippia*, as in Madagascar and Grande Comore. Apart from the occasional occurrence of *Monimia amplexicaulis*, *M. rotundifolia*, *Tambourissa crassa*, and *T. elliptica* subsp. *elliptica*, whose upper ranges end here, no species are specially adapted to the heath formation. Likewise, no species are known to be adapted to the semi-deciduous dry forest (“forêt mégatherme” of Cadet) in the island’s dry, leeward western sector (annual precipitation 800–1,500 mm).

In essence, Réunion’s extensive cloud forests have favored adaptive radiation in the genus *Monimia*, which comprises three of its five Monimiaceae species. *Monimia rotundifolia* is the most widespread and abundant species, constituting a woody element of major importance in the cloud forest zone. *Tambourissa*, with two species, has not undergone the extent of adaptive radiation here that has occurred in Mauritius and Madagascar, although seemingly suitable habitats exist. This may be attributable to its more recent arrival, or to the island’s younger age. That *Tambourissa* is undergoing adaptive radiation in Réunion is evident by the presence of two closely

related species, one with two subspecies occupying different ecological zones.

MAURITIUS

Geologically the oldest of the Mascarene Islands, Mauritius has probably undergone considerable reduction by erosion since its inception, being slightly smaller and only a third as high as Réunion. Since the island’s colonization by man almost 400 years ago, its original vegetation has been removed from nearly every accessible surface and has also undergone extreme degradation by introduced biota. Tracts representing most of the island’s original vegetation still remain, however, in the form of nature reserves and crown land which comprise ca. 5–6% of its superficies (Lorence, 1978). Unfortunately, virtually all have been invaded by introduced plants such as *Furcraea*, *Ligustrum*, *Psidium*, *Rubus*, and many others, not to mention introduced animals (monkeys, stag, pigs) and birds (sparrows, mynahs, bulbuls), which help spread seeds of the exotic plants. All are contributing to the inevitable disappearance of the remaining native flora and fauna (Vaughan, 1968; Siegfried & Temple, 1975; Jolly, 1982; Pasquier & Jones, 1982).

The majority of forested areas remaining in the uplands (precipitation 2,000–5,000 mm) are occupied by floristically rich wet forest of vari-

able composition but usually characterized by the presence of *Sideroxylon cinereum* Lam., *S. puberulum* A.DC., and other Sapotaceae such as *Labourdonnaisia* (the “*Sideroxylon* thicket” of Vaughan & Wiehe). Remnants of this formation extend down to ca. 200 m in some areas (e.g., at Bel Ombre) where up to three species of *Tambourissa* occur: *T. amplifolia*, *T. peltata*, and *T. tau* (Table 3; Figs. 38, 40).

In addition to the above, species such as *Tambourissa ficus* and *T. pedicellata* appear at higher altitudes, e.g., at Pieter Both Mt. (Table 3). Vaughan and Wiehe’s (1941) detailed study of the *Sideroxylon* formation at Perrier Nature Reserve revealed that two individuals of *Tambourissa peltata* and 16 of *T. tau* occurred in a 1,000 m² plot (Table 4), and family dominance at Perrier was only 0.47%, lowest of the three sites (Table 4). My survey of populations of these two species in the same area shows 26 individuals of *T. peltata* per 12,700 m² (= 21/ha) and 57 individuals of *T. tau* per 512 m² (= 1,113/ha) (Fig. 3). The higher figure for the latter species, an understory treelet, suggests aggregation into much denser populations than *T. peltata*, a more highly dispersed canopy tree. Population density of these two species appears to correspond to their pollinator strategies (see discussion under Floral Biology).

On parts of the upland plateau and in some sheltered valleys the *Sideroxylon* formation passes into a high forest (“climax forest” of Vaughan & Wiehe). Vaughan and Wiehe’s (1939, 1941) studies of the high forest at Macabé revealed the presence of 41 individuals 10 cm or more DBH belonging to three species of *Tambourissa* in a one hectare plot. In another 1,000 m² sample plot at Macabé, the genus was found to comprise 2.67% of the total number of individuals 10 cm or more DBH, with the following breakdown: *T. sieberi*, 13 (upper stratum tree); *T. ficus* (as *T. elliptica*), four (mid stratum tree); *T. pedicellata*, 28 (mid stratum tree; my survey in 1979 failed to show this species at Macabé); *T. tau* (as *T. amplifolia*), one (understory treelet). In addition, I found *T. amplifolia* to be a rare understory treelet or small tree at Macabé in 1979 (Table 3).

A comparable survey was carried out in somewhat drier high forest at Brise Fer (Table 3) several kilometers to the west of Macabé (Lorence et al., in prep.). Only two species of *Tambourissa* were found here, *T. ficus* and *T. peltata*, presumably due to the lower rainfall. Both showed up

TABLE 4. Comparative frequency of *Tambourissa* species in three uplant plant formations in Mauritius (adapted from Vaughan & Wiehe, 1941).

Species	Number Individuals per 1,000 m ²		
	<i>Philippia</i> Heath (Pétrin)	<i>Sideroxylon</i> Wet Forest (Perrier)	Macabé High Forest
<i>T. cordifolia</i>	44	—	—
<i>T. ficus</i>	—	—	4
<i>T. pedicellata</i>	—	—	28
<i>T. peltata</i>	1	2	—
<i>T. sieberi</i>	—	—	13
<i>T. tau</i>	—	16	1
Total	45	18	46
% Family dominance	2.04	0.47	2.67

in our study at the rate of two individuals 25 mm or more DBH per 1,000 m².

Because of the island’s low altitude, cloud forest only occurs on the flanks and summits of its highest mountains in areas of high rainfall (ca. 4,500–5,000 mm). In their study of the cloud forest (as “mossy forest”) on Mt. Cocotte, Vaughan and Wiehe (1937) recorded only two species of *Tambourissa* in a 40 m² transect: *Tambourissa sieberi*, three individuals; *T. tau* (as *T. amplifolia*), two individuals. My survey of the summit of Mt. Cocotte in 1979 (unpubl. data) revealed the presence of five additional species: *Monimia ovalifolia*, *Tambourissa cocottensis* (endemic to the mountain), *T. ficus*, *T. peltata*, and *T. tetragona* (also endemic to the mountain) (Table 3). Mt. Cocotte harbors the highest concentration of Monimiaceae in the entire island, with seven of its 11 species found here. A survey of the cloud forest on Mt. Lagrave revealed a comparable situation, with six species present.

Another consequence of the island’s low altitude is the paucity of *Philippia* heath formation in Mauritius, which occurs in small patches at only a few edaphically suitable areas such as Pétrin and Mt. Laselle. Formations of this type are restricted to areas of unweathered, highly ferruginous ground water laterite or “cuirasse,” so called because of its impermeability to water. Although receiving a high rainfall (4,000 mm at Pétrin), the laterite is nearly devoid of true soil, and the heath formation is exposed to constant drying winds. As a result, most woody species possess xeromorphic leaves (microphyllous, sclerophyllous, or variously pubescent).

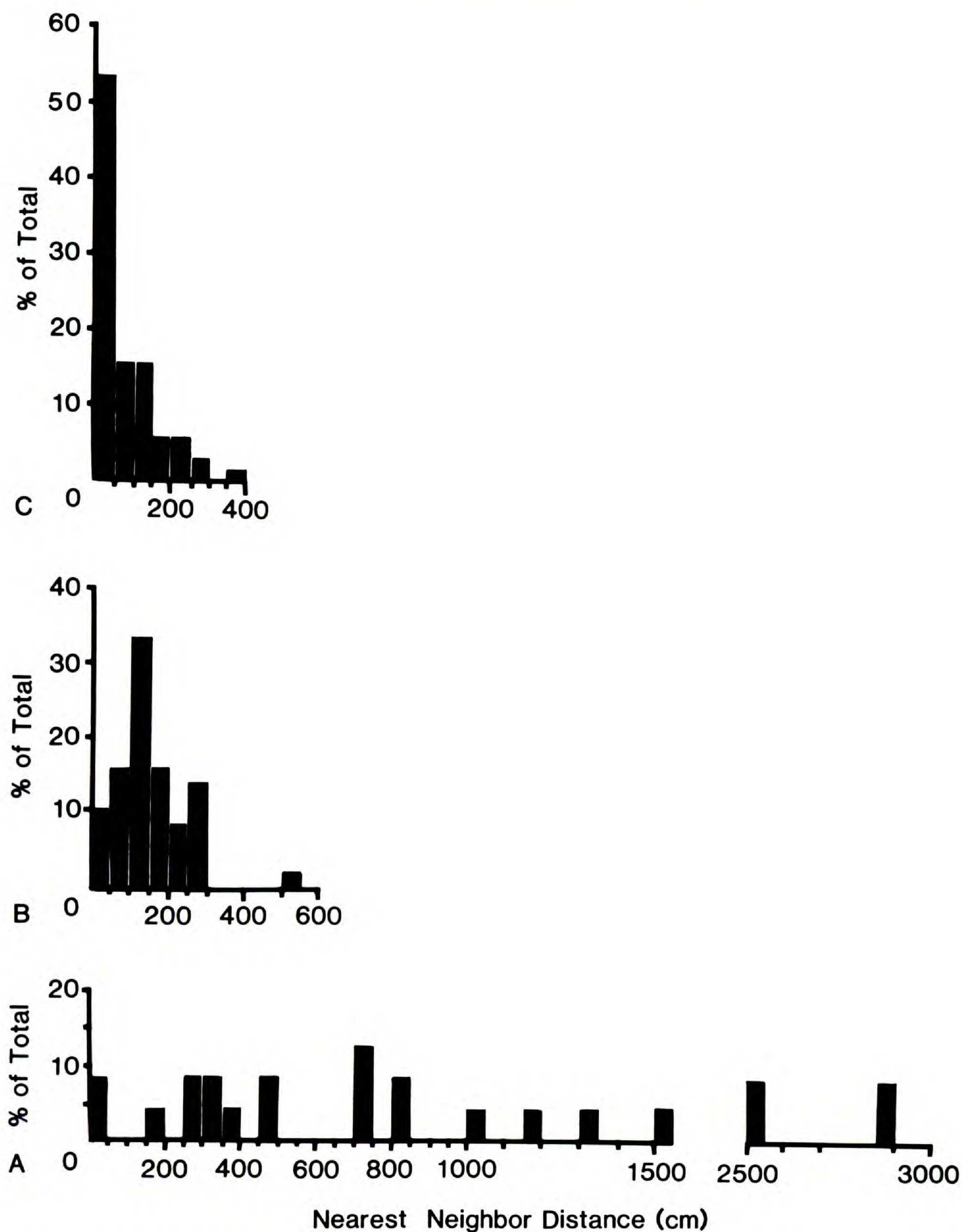


FIGURE 3. Nearest neighbor distance as percent of population for three species of *Tambourissa* studied in Mauritius, 1978–1979.—A. *T. peltata*, Perrier Nature Reserve, sample area = 12,700 m², N = 26 individuals, estimated frequency per hectare = 21.—B. *T. tau*, Perrier Nature Reserve, sample area = 512 m², N = 57 individuals, estimated frequency per hectare = 1,113.—C. *T. cordifolia*, Pétrin Nature Reserve, sample area = 410 m², N = 69 individuals, estimated frequency per hectare = 1,684.

Only a single species of Monimiaceae has successfully adapted to this environment: *Tambourissa cordifolia*, a low dioecious shrub with small, sessile coriaceous leaves. It is peculiar in being the only truly shrubby member of the genus known to me. In their study of a 1,000 m² tran-

sect at Pétrin, Vaughan and Wiehe (1941) found 44 individuals of *T. cordifolia*. My study of a population of the species at the same locality gave a much higher density (Fig. 3), 69 individuals per 410 m² (= 1,684/ha), suggesting the species is aggregated into dense, local popula-

tions. *Tambourissa cordifolia* also occurs in a few other regions with similar edaphic conditions, e.g., Mt. Laselle, Les Mares, and Mare Longue Plateau (Fig. 40).

Although *Tambourissa peltata*, and to a lesser degree *T. tau*, also occur in the heath formation at Pétrin, they are only marginally successful and occur as depauperate, stunted individuals. In their 1,000 m² sample, Vaughan and Wiehe (1941) only found a single individual of *Tambourissa peltata*, although I found it to be more abundant in localized areas. Family dominance for Monimiaceae in this habitat was 2.04% of the total individuals (Table 4), somewhat less than at Macabé but still a significant element of the woody flora (Vaughan & Wiehe, 1941).

Areas lying to the west of the central plateau, i.e., the western escarpment and lowland areas in the rain shadow (1,000–1,600 mm precipitation), experience a distinct dry season and support a semideciduous dry forest of Mauritius Ebony (*Diospyros tessellaria* Poir.), *Mimusops*, and *Elaeodendron* (Celastraceae). Of the island's ten species of *Tambourissa*, only *T. quadrifida* occupies this habitat to which it is restricted, e.g., at Yemen Valley (Table 3). The species occurs here as a mid stratum or canopy tree often forming small, localized populations.

Although many Monimiaceae readily sprout sucker shoots from cut stumps, no species were found to occur in secondary forests. Furthermore, regeneration of many is poor or lacking even in indigenous forest highly invaded by vigorous exotic species, suggesting that many should be considered as threatened species. For example, on Mt. Cocotte, which is heavily invaded by numerous exotics, only limited regeneration was observed in *Tambourissa ficus* and *T. peltata*, two of the commonest species. No signs of recent regeneration, however, were apparent in the rare and localized *T. cocottensis* and *T. tetragona*. However, vigorous regeneration of both *Tambourissa peltata* and *T. tau* was observed at Perrier Nature Reserve, which has been kept free of exotics for the last decade by a stringent weeding program carried out by the Forestry Department.

In summary, on one hand, Mauritius has favored the greatest adaptive radiation in *Tambourissa* of any of the satellite islands around Madagascar, probably as a result of its comparatively greater age coupled with the availability of a range of suitable habitats. *Monimia*, on the other hand, is represented by a single species confined to the island's few patches of cloud for-

est. Its poor representation may be attributable to a lack of suitable habitats or a relatively recent introduction.

RODRIGUES

Rodrigues, the smallest, most isolated, and possibly youngest of the Mascarene islands, only attains ca. 400 m maximum elevation and is the least diverse ecologically. As a result of its extreme isolation and paucity of suitable habitats, Monimiaceae appear to be absent from the island (e.g., Balfour, 1879; Wiehe, 1949; J. Guého, pers. comm.). A single collection of *Monimia ovalifolia* supposedly from Rodrigues is probably wrongly labelled (see discussion under the genus *Monimia*).

COMORE ARCHIPELAGO

The Comores are poorly known botanically but appear to harbor predominantly African and Madagascan floristic elements (Voeltzkow, 1917). Of the four islands, information is available only for Grande Comore (Legris, 1969) in the form of a survey of vegetation types and enumeration of their most common and conspicuous elements.

GRANDE COMORE

Grande Comore, youngest of the islands, has virtually no intact lowland forest remaining. Areas of well-developed lower montane wet and montane cloud forest still remain on the lower windward and mid altitude slopes beginning at ca. 500–800 m, however, notably on the Karthala volcano and La Grille massifs where annual precipitation ranges from ca. 3,000 to 5,000 mm (Legris, 1969). Of recent volcanic origin, the La Grille massif supports mature wet forest dominated by large individuals of *Weinmannia*, *Anthocleista*, *Eugenia*, and *Macaranga* attaining ca. 20–30 m, and also harbors the island's only species of Monimiaceae, *Tambourissa comorensis*. One of the largest members of the genus, it appears to be restricted to La Grille where it constitutes an important element of the forest, conspicuous because of its numerous large, brown cupuliform fruits hanging from the trunk and major branches (Fig. 17B).

Wet forest on the Karthala volcano massif is dominated by *Ocotea*, *Nuxia*, *Olea*, and *Aphloia*, but no Monimiaceae have been noted or collected there to my knowledge. A cloud zone often

forms above ca. 1,000 m. At ca. 1,800–2,000 m the wet/cloud forest zone on Karthala gives way to an ericoid heath formation of *Philippia* similar to that in Madagascar and Réunion; no Monimiaceae are known from this zone.

The leeward western region of the island probably once supported dry forest, of which huge baobabs (*Adansonia digitata* L.) and other scattered trees are the only remnants. No Monimiaceae are known from this zone either.

ANJOUAN

Unfortunately, I was unable to visit Anjouan, which is extremely poorly known botanically. Most of its lowland forest has been destroyed, although the mountainous central massifs (e.g., N'Tingui) support fairly extensive areas of wet and cloud forest due to their rugged relief (I. Tattersall, pers. comm.). Two species of *Tambourissa*, *T. kirkii* and *T. paradoxa* (syn. *T. johannae*) are known from Anjouan, but little is known of their ecology and distribution. Both apparently occur in the wet and cloud forest zones (Fig. 35). Although Anjouan only attains ca. 1,600 m, it may harbor small amounts of heath vegetation on its highest peaks. Dry forest probably occurred on its dry, lower leeward slopes as is the case for Mayotte and Grande Comore.

MOHÉLI

Mohéli, smallest of the Comores, is also virtually unknown botanically. Although I was unable to visit it, I. Tattersall (pers. comm.) stated that several extensive areas of montane wet forest still remain on its central ridge at Mt. St. Antonio, and between Fomboni and Drondoni (ca. 500–700 m elevation). Collections from these areas made by L. Bernardi in 1967 have revealed the presence of a new endemic species of *Tambourissa*, *T. moheliensis*, and apparently the only one to occur there. Little is known of its distribution and ecology (Fig. 35). Most of Mohéli's lowland vegetation is now gone. Presumably wet forest occurred on the windward slopes and dry forest on the lower slopes in the rain shadow, as is the case for Mayotte and Grande Comore.

MAYOTTE

Oldest and lowest of the Comores, Mayotte supports only a few small areas of indigenous forest, the rest being cultivated or secondary in

nature. Several of the island's highest mountain massifs, i.e., Benara (650 m) and Hachiroungou (500 m), support wet forest dominated by *Nuxia*, *Aphloia*, and *Macaranga* similar to that found on Grande Comore. Occasional local populations of the Mayotte's only Monimiaceae species, *Tambourissa leptophylla*, still occur here (Fig. 35). A number of large mature individuals and signs of recent regeneration were observed on Benara. *Tambourissa leptophylla* also occurs sporadically as a remnant in wet lowland secondary forest at Barakani and Sada. In the dry, western leeward region remnants of dry forest with *Adansonia digitata* occur on isolated peaks and offshore islets. No Monimiaceae were found to occur there.

In essence, although each of the Comores supports its own single endemic species of *Tambourissa* (two in Anjouan), adaptive radiation of the genus here has been less extensive than in the Mascarenes or Madagascar. As habitat diversity in the Comores is roughly comparable to that in the Mascarenes in spite of their smaller average size, the low *Tambourissa* species diversity may be due to the islands' relative youth or possibly a more recent date of introduction of the genus. That four of the five Comorean species appear to be closely related, and that all species for which data are available are restricted to the wet/cloud forest zone (none are adapted to either dry forest or heath formation), suggests a relatively short history for *Tambourissa* in the Comores.

This review of the ecology and distribution of the Monimiaceae in the Malagasy region demonstrates that members of the family are floristically important constituents of the islands' plant formations. Furthermore, the various species have different life forms ranging from shrubs or understory treelets to mid stratum or even canopy trees. The family attains its greatest diversity and abundance in the lower montane wet and montane cloud forest zones, although a significant number of species are adapted to the lowland wet forest zone. Only a few species are adapted to the high altitude heath formation and the semideciduous dry forest, however. Although many species of *Tambourissa* have the ability to form coppice shoots from cut trunks, they are virtually absent from secondary vegetation and exhibit a poor ability to regenerate when competing with vigorous, invasive exotic species.

MORPHOLOGY AND ANATOMY

Because they are generally considered to be a key family for the critical interpretation of a number of other Lauralean families (e.g., Chloranthaceae, Gomortegaceae, Hernandiaceae, and Lauraceae), the Monimiaceae have been relatively well studied morphologically and anatomically (Baillon, 1871; Hobein, 1889; Perkins, 1898, 1925; Perkins & Gilg, 1901; Metay, 1921; Garratt, 1934; Money et al., 1950; Lemesle & Prichard, 1954; Sampson, 1969a, 1969b, 1969c; Endress, 1972, 1980a, 1980b). However, apart from a few species in the genera *Monimia*, *Tambourissa*, and to a lesser degree *Decarydendron*, the species in the Malagasy area have not been well studied morphologically or anatomically.

METHODS AND MATERIALS

Gross morphological observations were made from herbarium specimens and collections preserved in alcohol. For venation studies, dried leaves were rehydrated, cleared in KOH, bleached, stained in safranin, dehydrated, and mounted in Permout resin between glass plates according to the method of Dilcher (1974). Prints of venation patterns were made using a photographic enlarger and standard photographic print paper (f3, f4, or f5). Leaf trichomes were prepared for the SEM by Au-Pd sputter-coating and photographs were taken on a Cambridge Stereoscan Mark II. Material for floral anatomical studies was fixed in alcohol or FAA (*Monimia*, most *Tambourissa*), or dried herbarium material was restored in 5% NaOH (*Decarydendron*, *Ephippiandra*) after which it was dehydrated in a TBA series, embedded in Paraplast, sectioned on a rotary microtome, dewaxed and stained with safranin and fast green, and mounted according to methods in Jensen (1962). In some cases, carpels were cleared in KOH, stained, dehydrated, and mounted in Permout to observe the vasculature.

HABIT AND BARK

Monimiaceae in the Malagasy region are mostly understory to mid stratum treelets or small trees, or large canopy trees. I know of no species that occur as emergents. The shrubby habit is quite rare, and no true vines are known from the region. The boles of all species I have observed were cylindric, often with knobby meristematic swellings in the cauliflorous species. The trunk

is basally swollen in *Tambourissa ficus*, *Tambourissa longicarpa*, and *Decarydendron perrieri*, where the flowers are generally produced. None of the species are known to have buttresses or prop roots.

Species of *Monimia* are small- to moderate-sized mid stratum or canopy trees, often shrubby when growing in exposed habitats. Both *M. amplexicaulis* and *M. rotundifolia* reach ca. 10 m tall, whereas *M. ovalifolia* is known to attain 15 m. Trunks of old individuals of all three species are often somewhat reclining and may reach diameters of 30–40 cm in *M. amplexicaulis* and *M. ovalifolia*, and up to 60 cm in *M. rotundifolia*. The bark is generally pale brown or reddish brown, soft, smooth, and flakes off in patches. Because the species are confined to very humid habitats, the bark is often overgrown with bryophytes and other epiphytes.

Of the Madagascan endemic genera, *Decarydendron* and *Ephippiandra* are shrubs, treelets or trees to 10–25 m tall (e.g., *E. madagascariensis* and *E. tsaratanensis*). No information is available on the boles or bark of these two genera.

Tambourissa includes species with a wide range of woody life forms ranging from shrubs rarely exceeding a meter (*T. cordifolia*) to large canopy trees 10–20 m tall (e.g., *T. comorensis*, *T. sieberi*). The majority of species, however, are understory treelets (e.g., *T. amplifolia*, *T. tau*) or small mid stratum trees (e.g., *T. ficus*, *T. purpurea*). The only reportedly vining species is *T. madagascariensis*, a “lianescent shrub” (*Rababoto sub RN 6028*, P), which may also be a large tree 15 m tall (*Anon. sub herb. Alaotra 2126*, MAD). Except for the shrubby *T. cordifolia*, most species are monocaulescent, although many are capable of forming multiple stems from coppice shoots (e.g., *T. cocottensis*, *T. tau*, *T. quadrifida*), after death of the main stem.

Although often licheniferous or covered with bryophytes, the bark of most species of *Tambourissa* is pale grayish or brownish, soft and corky, smooth to longitudinally fissured, and flakes or peels off in strips or patches. For the 16 species examined, characteristics of the slash (an oblique cut through the outer and inner bark) include a beige or pale pink to salmon-colored inner bark (phloem), and whitish or straw colored wood (xylem), both showing the conspicuous wide rays characteristic of many Monimiaceae. No sap or exudate was apparent.

In summary, the Malagasy area Monimiaceae

are treelets or trees most abundant in the canopy and lower strata of tropical forests. Only a small number of species have shrubby or lianescent habits. The bark of *Monimia* and many species of *Tambourissa* is relatively uniform, but needs further study in *Decarydendron* and *Ehippiandra*.

WOOD ANATOMY

Anatomical studies of the wood of representative genera and subfamilies of Monimiaceae conducted by Garratt (1934), Money et al. (1950), and Lemesle and Prichard (1954) reveal a number of trends of specialization. Most striking are progressive changes in the vessel members which include a shortening and broadening, a decrease in the degree of end wall overlapping, and a transition from scalariform to simple perforation plates.

Of the four genera examined from the Malagasy area (Money et al., 1950), *Decarydendron*, *Ehippiandra* (as *Hedycaryopsis*), and *Tambourissa* (all Mollinedioideae sensu Thorne) possess wood anatomical features interpreted as being relatively unspecialized within the family. These include long, thin-walled vessel members with angular, extensively overlapping end walls, and in *Tambourissa* (the only genus for which mature wood was available) scalariform perforation plates (Garratt, 1934; Money et al., 1950).

The xylem of *Monimia* (Monimioideae sensu Thorne) exhibits a number of trends that have been interpreted as advanced within the family (Money et al., 1950). Vessel members of *M. ovalifolia* are relatively short with somewhat obtuse end walls that do not overlap extensively and have perforation plates transitional between scalariform and simple porous. In this respect, specialization in the xylem of *Monimia* (and also *Palmeria*—Mollinedioideae) has attained a level comparable to that of *Peumus* (also Monimioideae), also with simple perforation plates.

Common wood anatomical features shared by both the Monimioideae and the Mollinedioideae are: scanty wood parenchyma; rather broad, multiseriate rays; presence of septate fibers; presence of fibers and hippocrepiform sclerids in the stem pericycle (Money et al., 1950).

STEMS AND PHYLLOTAXY

Adult phyllotaxy in *Monimia*, *Decarydendron*, *Ehippiandra*, and most species of *Tam-*

bourissa is opposite to subopposite and decussate. The three *Tambourissa* species in species Group 8 have ternate to subalternate adult leaves (Table 1), although seedlings of two, *T. ficus* and *T. peltata*, have opposite decussate leaves. On the other hand, adult leaves of species which are normally opposite are sometimes ternate on vigorous sucker shoots (e.g., *Monimia ovalifolia*, *Tambourissa purpurea*, and *T. pedicellata*). Although opposite and decussate, the adult leaves of *T. tau* (Fig. 39A) are unique in being clustered into pseudoverticels of two to four pairs, separated by long "internodes." Phyllotaxy is generally a constant, species-specific feature.

Leafy stems of most species of all four genera are more or less terete with flattened, somewhat dilated nodes. *Tambourissa tetragona* is unique in having winged, quadrangular stems, whereas those of the ternate leaved species (Group 8) are somewhat trigonous.

Stems of *Decarydendron*, *Ehippiandra*, and most *Tambourissa* species bear sparse to dense, straight or undulate, simple or rarely fasciculate (e.g., *T. comorensis*, *T. mohelensis*) lignified trichomes. In a few species even the new growth is virtually glabrous (e.g., *T. cocottensis*, *T. cordifolia*, and *T. tetragona*). In *Monimia*, the stems are scabrous to velutinous with an indument of stellate, fasciculate and simple trichomes. Lenticels often occur on the stems of certain species (e.g., *T. ficus*, *T. peltata*, *E. perrieri*, *E. domatiata*, and *E. myrtoidea*) but are absent in most. Stem characters thus provide a number of species-specific, taxonomically useful features.

Monimia, *Decarydendron*, *Ehippiandra*, and *Tambourissa* all characteristically possess multiple axillary buds of which I found no mention in the literature. In all three species of *Monimia* (as in *Peumus*), three horizontally oriented buds are usually present in each leaf axil, the central one being largest and developing first (if at all). The vegetative buds have small, pubescent scales, whereas those enclosing the inflorescence are large, brown, and subglabrous. In the remaining genera, all Mollinedioideae, the buds are oriented longitudinally in the leaf axil, the central one usually being largest and the first to develop (if at all). On flowering branches of the ramiflorous species *E. madagascariensis* and *E. tsaratanensis* there are three to five buds, the central one usually giving rise to the inflorescence and the lateral ones to vegetative shoots. In *D. helenae* var. *stenophyllum* the buds occur in groups of three, whereas in *E. microphylla* and *E. myrtoid-*

ea they are solitary or in pairs. Three, less commonly two, axillary buds are present in nearly all species of *Tambourissa* examined, regardless of whether the inflorescence is terminal, ramiflorous or cauliflorous. On flowering stems of ramiflorous species such as *T. purpurea*, the large central bud frequently but not invariably gives rise to the inflorescence. On vegetative stems, the central bud usually develops first, although two buds may occasionally develop into vegetative shoots simultaneously. *Tambourissa tetragona* is exceptional in that only one bud is obvious. However, vigorous sucker shoots of *T. ficus* may produce up to six buds extending in a row for several centimeters above the leaf axil (Lorence 2235, MO).

LEAVES

The terminology used to describe leaves in this monograph follows Hickey (1973, 1977), Hickey and Wolfe (1975), and to an extent Lawrence (1951). Leaves of all Monimiaceae are exstipulate, considered by Hickey and Wolfe (1975) to be an advanced condition within the Laurales. Characters of the petiole and lamina, including size and shape, margin, venation, and pubescence, provide a series of taxonomically useful features in many taxa.

Petiole. The leaves of most genera and species have a well-differentiated lamina and petiole, but *Monimia amplexicaulis* (Fig. 4A) and *Tambourissa cordifolia* (Fig. 8B) are unique in having sessile cordate, amplexicaul leaves. Petioles of most other species are slender to stout, of variable length but much shorter than the lamina, and are adaxially flattened or canaliculate. They are either glabrous or bear an indument of trichomes similar in type and density to that of the stem internodes. In all three species of *Monimia* (*M. amplexicaulis*, Lorence 2503, MO; *M. ovalifolia*, Lorence 1857, MO; *M. rotundifolia*, Lorence 2472, MO), the vascular strands of the petiole are united into an adaxially flattened cylinder (see also Money et al., 1950). In the other genera which I examined (*Ehippiandra myrtoidea*, Baron 1355, K; *E. madagascariensis*, Bernardi 11977, MO), and six species of *Tambourissa* (*T. cocottensis*, Lorence 2287, MO; *T. crassa*, Lorence 2767, MO; *T. elliptica* subsp. *micrantha*, Lorence 2488, MO; *T. ficus*, Lorence 2162, MO; *T. pedicellata*, Lorence 2385, MO; and *T. tetragona*, Lorence 2286, MO), the petiolar vascular strands are aggregated into a shallow, U-shaped

arc. This corresponds with Metay's (1921) findings for *T. floricosata* (as *Schrameckia madagascariensis*) and *T. thouvenotii*.

Lamina. Leaves of *Monimia* are subcoriaceous to coriaceous, usually ovate to elliptic or suborbiculate, and their size and shape are generally much more polymorphic in *M. ovalifolia* and *M. rotundifolia* than in *M. amplexicaulis*. Although the extreme forms appear to be very distinct (Fig. 4), leaf size and shape in *Monimia* do not provide stable taxonomic features. Likewise, shape of the apex is quite variable (acuminate, acute, or obtuse) and of little taxonomic importance in all three species. Characters of the leaf base, however, are useful in distinguishing *M. amplexicaulis*, where it is deeply cordate and amplexicaul, from the other two species where it ranges from shallowly cordate to rounded, obtuse, acute or decurrent (Fig. 4).

Leaves of the three species of *Decarydendron* do not differ markedly from each other, ranging from elliptic to oblong or obovate. The texture is chartaceous to subcoriaceous, the apex acute or acuminate, and the base cuneate.

Leaves of the six species of *Ehippiandra* are small- to medium-sized and chartaceous to coriaceous in texture. Laminar shape is generally characteristic for each species: ovate or elliptic with acute or acuminate apices and cuneate to rounded bases in *E. microphylla* and *E. myrtoidea* (Fig. 6A); elliptic with a retuse apex folded downward into a flap in *E. perrieri* (Fig. 6B); obovate-elliptic to rhombic and apiculate in *E. domatiata*; orbicular with an obtuse to truncate base and obtuse to rounded apex in *E. madagascariensis* and *E. tsaratanensis*. (Fig. 6E, F).

The 43 species of *Tambourissa* display a wide array of leaf morphologies which are relatively constant and species-specific. In widespread species with a broad ecological amplitude (e.g., *T. peltata*, *T. purpurea*), considerable intraspecific variation occurs in size and shape, generally between populations growing in different habitats. Texture ranges from membranaceous in *T. leptophylla* to coriaceous in *T. parvifolia* and *T. religiosa*. Size varies from small in *T. parvifolia* (attaining only 47 mm by 22 mm) which grows in high altitude montane forest, to very large in *T. amplifolia* (attaining 500 mm by 240 mm) which grows in lowland wet forest. Leaf shape varies considerably within many species but in others it is of considerable taxonomic significance, e.g., in distinguishing the two subspecies of *T. elliptica*. Leaf shape in the genus ranges

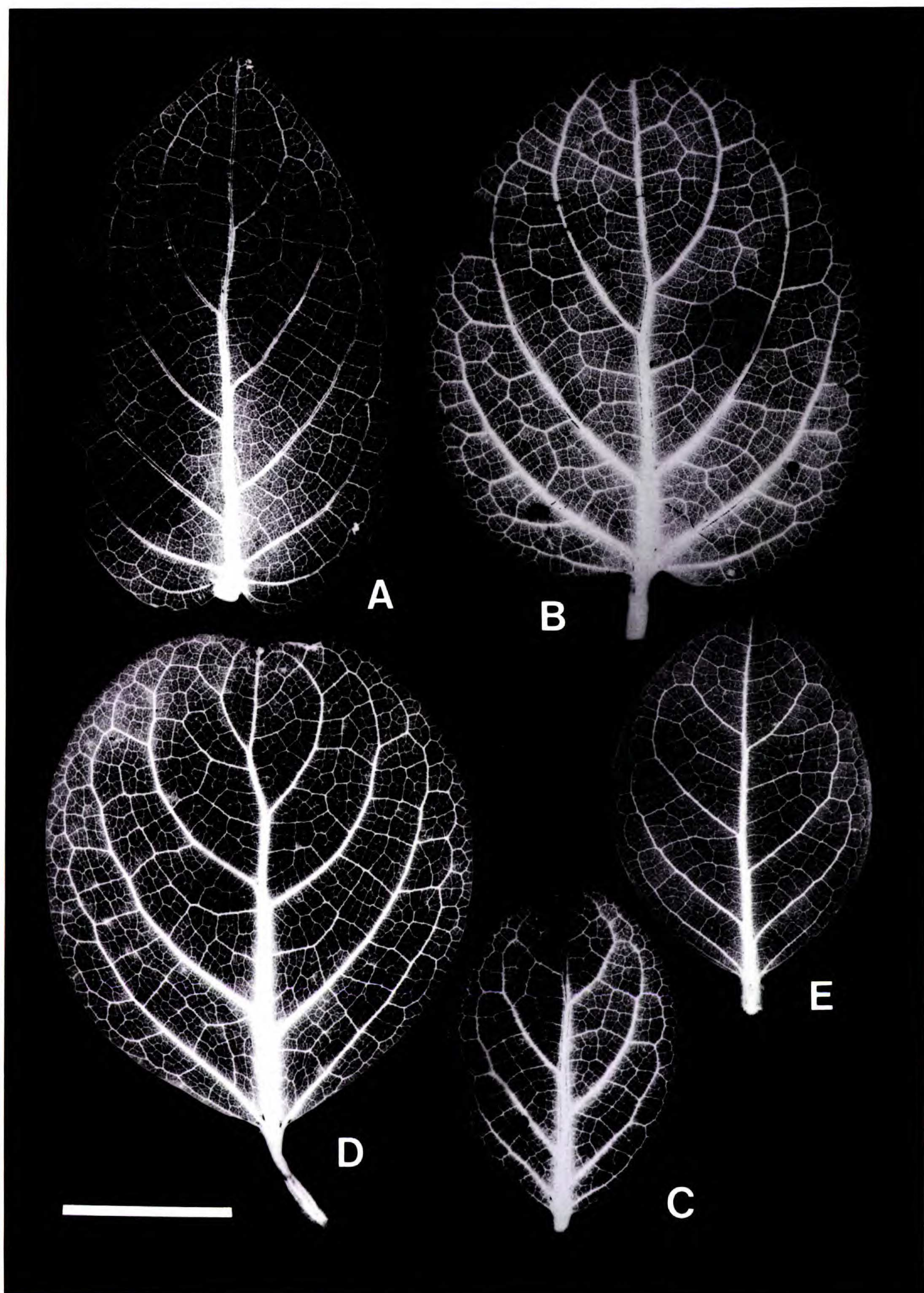


FIGURE 4. Leaf clearings of *Monimia*.—A. *M. amplexicaulis*, Rivals s.n. (TL-R).—B. *M. rotundifolia*, Rivals s.n. in June 1943 (TL-R).—C. *M. rotundifolia*, Bosser 21332 (P).—D. *M. ovalifolia*, Cordemoy s.n. (TL-R).—E. *M. ovalifolia*, Guého sub MAU 14130 (MAU). Bar equals 25 mm.

from cordate or ovate to elliptic, oblong, or obovate.

Studies of leaf anatomy in *Monimia* and *Tambourissa* (Hobein, 1889; Metay, 1921) show their laminar structure to be similar to that of many bifacial dicot leaves. The two species of *Monimia* and six species of *Tambourissa* examined by them all have a cuticle, an upper epidermis, a hypodermis consisting of one to six cell layers, a mesophyll differentiated into a palisade layer one or two cells thick and a spongy layer many cells thick, and a lower epidermis also covered by a cuticle. Stomata are restricted to the lower epidermis in all species except *T. thouvenotii*, which also has stomata in the upper epidermis (Metay, 1921).

Leaves of Monimiaceae are characterized by the presence of spheroid laminar glands or secretory cells containing so-called "ethereal" oils which impart a particular odor to many species. In most species of *Tambourissa* these are concentrated in the mesophyll, but lesser numbers also occur in the lower epidermis and hypodermis (Hobein, 1889; Metay, 1921). Hobein (1889) stated that both *Monimia ovalifolia* and *M. rotundifolia* have secretory cells restricted to the hypodermis and not in the mesophyll as in *Tambourissa* and the other genera he studied. My investigations of hand sectioned, alcohol fixed leaves show that secretory cells are restricted to the hypodermis only in *M. ovalifolia*, both in plants from Mauritius (Lorence 1857, 2896, MO) and from Réunion (Lorence 2757, MO). In *M. amplexicaulis* (Lorence 2503, MO) and *M. rotundifolia* (Lorence 2472, MO), secretory cells were found to occur not only in the hypodermis, but also in the interface between the palisades and spongy mesophyll. An examination of sections of restored leaves of *Decarydendron heleanae* var. *stenophyllum* (Humbert 6613, K), *Ehippiandra tsaratanensis* (Gentry 11605, MO), and *E. myrtoidea* (Baron 1263, K) shows that they are fundamentally similar to species of *Tambourissa* anatomically.

Venation and margin. The Monimiaceae possess several distinctive trends which Hickey and Wolfe (1975) consider to be advanced within the Laurales, notably development of the Monimioid tooth with an unbraced medial vein and an indurated cap, and secondary veins originating at uniform angles to the costa.

All three species of *Monimia* possess stoutly brochidodromous venation of the festooned type characteristic of the family. Three to four pairs

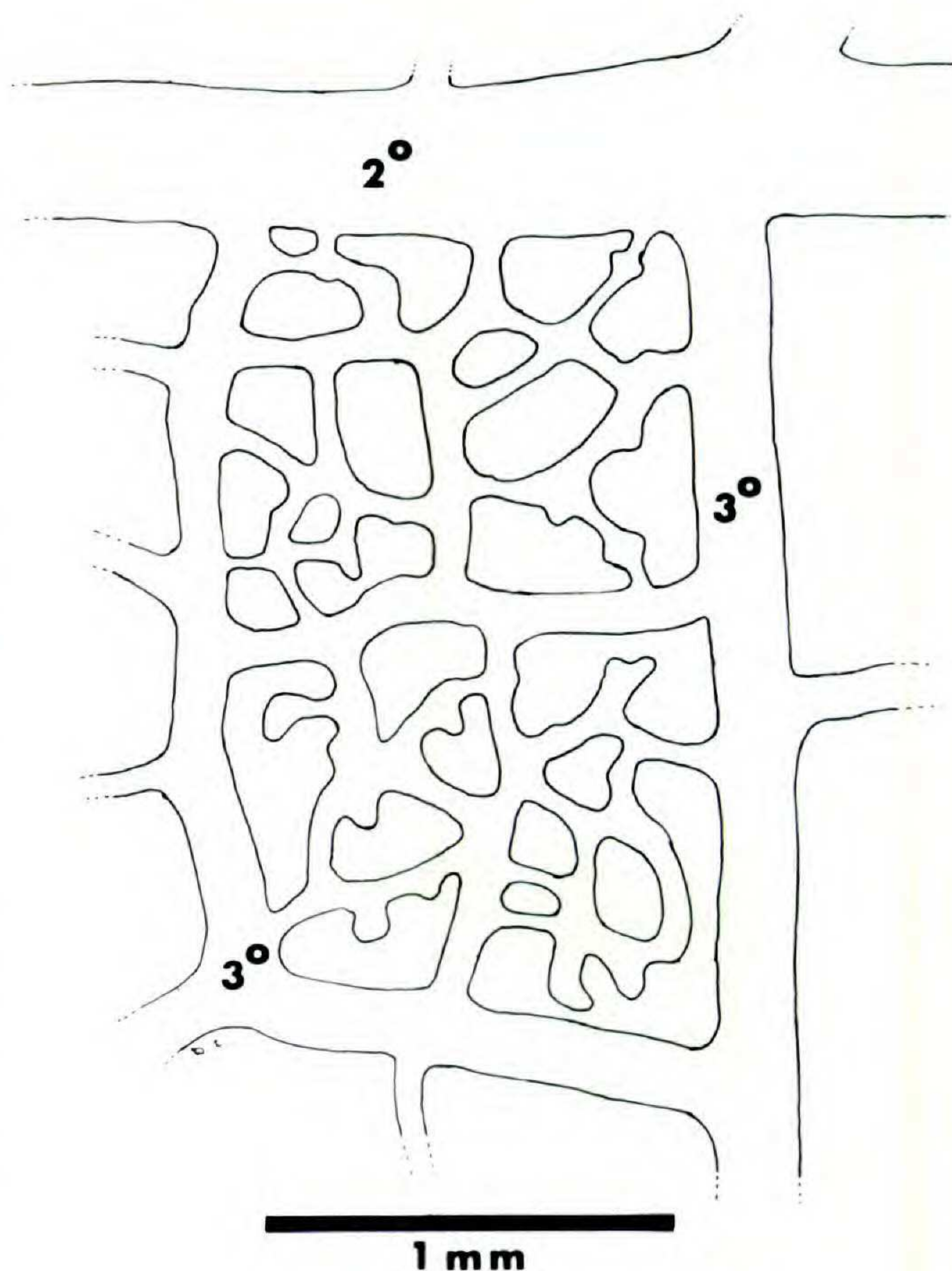


FIGURE 5. Camera lucida drawing of ultimate venation in cleared leaf of *Monimia ovalifolia*, Bijoux sub MAU 1310 (MAU). 2° = secondary venation, 3° = tertiary venation.

of secondary veins originate at comparatively uniform angles, are bowed to geniculate, follow a regular, slightly sinuous course and delimit relatively regular and uniform intercostal areas (Fig. 4A–E). Consequently, all three species fall into Hickey's (1977) second rank leaf category. Distally the secondaries continue to form another, higher order of loops characteristic of the festooned brochidodromous venation pattern (Hickey & Wolfe, 1975). The numerous intermarginal loops of the last order unite to form a weak, fimbriate intramarginal vein generally lacking in the other genera.

Intercostally, the tertiary veins originate at right angles from the secondaries and their arches and unite to form a series of strong, transverse tertiaries which in turn ramify at right angles and then anastomose admedially to form composite intersecondaries that usually follow a zig-zag course. These tertiary areoles are generally orthogonal (rectangular or pentagonal) and much more regular than in the other genera (Figs. 4, 5). The quaternaries arise from the tertiaries at nearly right angles to form fairly regular rectangular areoles. Vein orders above the quater-

nary are generally indistinct and ramify to form a reticulum of irregular areoles with included veinlets that anastomose or remain free (Fig. 5). Terminal idioblasts appear to be absent from the veinlets. The number and pattern of veins in *Monimia* provide few characters useful in separating the species, although they are characteristic of the genus as a whole.

Adult leaves of all three *Monimia* species have entire, generally slightly revolute margins. Seedling leaves of *M. ovalifolia* and *M. rotundifolia* (unknown in *M. amplexicaulis*) are also entire, as opposed to those of *Tambourissa* (D. Lorence, pers. observ.) and *Hortonia* (Endress, 1980a) which are generally dentate. Although the Monimioid tooth is, ironically, absent in *Monimia*, its venation is highly organized and appears to be advanced in this respect. The genus may possibly have undergone loss of teeth secondarily, as appears to be the case for *Tambourissa*.

Venation in all three species of *Decarydendron* is festooned brochidodromous. The six to 12 pairs of secondaries arise at quite constant angles, delimit regular intercostal areas, and continue to loop for several orders. Tertiary veins arising inside the secondary arches ramify admedially to form a reticulum of irregular areoles as they descend obliquely across the intercostal area. The quaternaries arise from the tertiaries at irregular angles and delimit irregular areoles. Vein orders above the quaternary are indistinct, and probably ramify to form free, included veinlets. Adult leaves of all three species of *Decarydendron* are serrate-dentate along the greater portion of their plane margins, each tooth ending in an indurated cap. An unbranched distal excurrent vein arising from the outer series of brochidodromous arches runs directly into each tooth. In this respect the venation is not truly semicraspedodromous according to Hickey's (1973) definition.

Species of the genus *Ehippiandra* (including *Hedycaryopsis*) display a distinctive trend from festooned brochidodromous to specialized and highly organized semicraspedodromous and craspedodromous patterns, the latter unknown elsewhere in the family. Leaves of *E. microphylla*, *E. myrtoidea*, and *E. perrieri* are small with only four to six pairs of secondary veins which unite into arches near the margin, and the festooning is often weak (Fig. 6A, B). Several tertiary veins arise on the distal parts of the secondary arches and descend parallel to the secondaries or somewhat obliquely across the intercostal areas, often ramifying into strongly

admedial branches as they approach the costa. The tertiaries delimit irregular intercostal areas in *E. myrtoidea*, but these are more regular and orthogonal in *E. perrieri*. Higher vein orders above the tertiary are not very distinct and generally form a more or less random reticulum of irregular areoles, ultimately terminating in free, dendroid veinlets lacking idioblasts. Margins are entire and somewhat revolute in *E. myrtoidea* and *E. perrieri*, but those of *E. microphylla* generally have a single pair of small teeth in the apical portion arising from exmedial branches of the secondary arches.

Leaves of *E. domatiata* (Fig. 6C, D) are likewise small with two to three pairs of secondaries, but show certain modifications towards the semicraspedodromous pattern. Although the weak basal pair of secondary veins forms a series of festooned loops in the customary brochidodromous manner, the second, stronger pair ascends for over half the lamina's length before joining the next pair above. On each side of the lamina one of the secondary branches runs directly into the margin, terminating in a small tooth. The tertiaries delimit fairly irregular intercostal areas, although the quaternaries form more regular areoles with free, branching veinlets. The margin is moderately revolute, and it is the only species known to have barbate domatia in the basal secondary vein axils, hence the specific epithet.

Ehippiandra tsaratanensis (Fig. 6E) has much larger, broader leaves which show a weakening of the brochidodromous pattern and the formation of sunken marginal teeth. As each of the four to seven pairs of secondary veins bifurcates, each branch generally unites with an adjacent branch to form a weak arch whose exmedial portion in turn gives rise to one or more distal branches. Each of these runs to the margin where it terminates in a rounded, centrally depressed tooth. The intersecondary webbing pattern of the tertiaries is stronger than in the preceding species, with more regular orthogonal, often quadrangular, tertiary areoles frequently bisected by zigzagging admedial branches. The quaternaries form generally small, more or less orthogonal areoles with free, included branched veinlets.

Leaves of the sixth species, *Ehippiandra madagascariensis* (Fig. 6F) are the most highly specialized of all, being almost orbicular with four to five pairs of secondary veins forming an open, craspedodromous pattern due to a further weakening of the secondary arches. Each secondary departs from the costa at a uniform angle

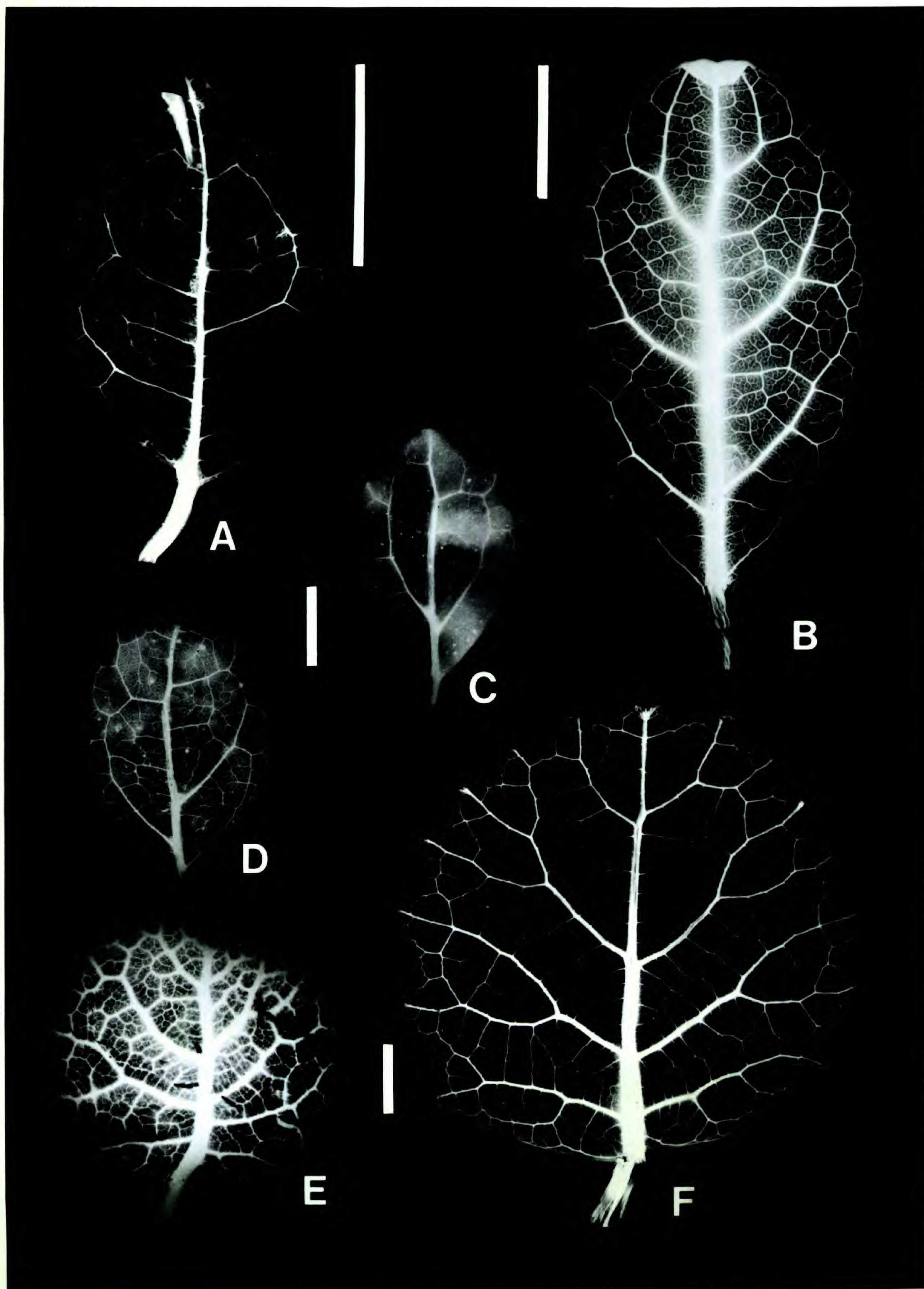


FIGURE 6. Leaf clearing of *Ehippiandra*.—A. *E. myrtoidea*, Baron 1355 (K).—B. *E. perrieri*, Morat 2332 (MAD).—C, D. *E. domatiata*, Capuron 8828-SF (P).—E. *E. tsaratanensis*, Gentry 11605 (MO).—F. *E. madagascariensis*, Bernardi 11977 (MO). Bars equal 10 mm.

and generally bifurcates once or rarely twice before the (usually basal) branch terminates in a single, depressed tooth as in the previous species. Occasionally, an apical sub-branch unites with a superadjacent secondary. As in the latter species, the tertiaries form a strong intersecondary cross webbing pattern delimiting regular intercostal areas. The tertiaries nearest the costa frequently display a strongly admedial zigzag branching pattern, whereas the quaternaries generally form irregular areoles with highly branched, free included veinlets as in the other species. The margin of *E. madagascariensis* is sinuate-dentate with seven to nine pairs of sunken teeth, including one at the apex, as in the preceding species. These teeth contain terminal tracheary elements and appear to be hydathodal.

A situation analogous to that in *Ehippiandra* occurs in *Hibbertia* (Dilleniaceae). Rury and Dickson (1977) explain the ontogenetic transitions in *Hibbertia* as follows:

"The craspedodromous venation pattern appears to be (in most cases) the result of an ontogenetic modification of the weakly brochidodromous pattern. Semicraspedodromous venation apparently resulted from formation and subsequent vascularization of marginal teeth in leaves with weakly brochidodromous venation. The tooth vasculature arises exmedially from the brochidodromous arch in leaves of *Hibbertia cuneiformis*, etc."

This same transition is apparent in the six species of *Ehippiandra*: a weakening and opening of the brochidodromous pattern with subsequent vascularization of the teeth from the secondary branches. This transition from weak brochidodromy to simple craspedodromy could result from a differential thickening of the portion which connects the basal part of the secondary arch with the marginal tooth, which can be seen in the basal veins of *E. madagascariensis*. According to Rury and Dickson (1977), Hickey (pers. comm.) stated that the ontogenetic transition from semicraspedodromy to simple craspedodromy has resulted from such a shift in vein development in many dicot leaves.

Tambourissa species (including *Phanerogonocarpus*) have venation patterns based on the festooned brochidodromous theme. Number of secondary veins ranges from three or four pairs (e.g., *T. parvifolia*, Fig. 8C; *T. elliptica* subsp. *elliptica*, Fig. 7D; *T. thouvenotii*, Fig. 7A), to six to 12 pairs in *T. elliptica* subsp. *micrantha* (Fig. 7E). The secondaries are stout, straight or sinuate, and delimit intercostal areas which may be ir-

regular (*T. thouvenotii*, Fig. 7A), or quite regular (*T. elliptica* subsp. *micrantha*, Fig. 7E; *T. cordifolia*, Fig. 8B). Species with fewer secondary veins frequently have less regular intercostal areas; some of these approach Hickey's (1977) "first rank" leaf category in this respect (e.g., *T. thouvenotii*, Fig. 7A). The majority of species, however, fall into his "second rank" category. In these, the secondaries from a fairly strong series of brochidodromous arches and continue to loop or festoon for several orders. The ultimate exmedial series of loops is often irregular and discontinuous (e.g., *T. leptophylla*, Fig. 8E), and does not form a true marginal fimbrial vein, although the strong intramarginal loops of *T. religiosa* resemble a fimbrial vein (Fig. 8D). The tertiary veins arise at wide acute to slightly obtuse angles from the secondaries and their arches, and are often admedially and obliquely ramified, forming strong, composite intersecondaries (e.g., *T. elliptica* subsp. *micrantha*, Fig. 7E). Tertiary areoles are generally irregular, although orthogonal areoles may be delimited by transverse tertiaries in some species with more highly organized venation (e.g., *T. peltata*, Fig. 8A; *T. elliptica* subsp. *elliptica*, Fig. 7D). Higher order veins are generally indistinct above the quaternary and sometimes tertiary levels. The quaternaries generally ramify and anastomose to form irregular areoles with dendroid, highly branched, free included veinlets. Terminal idioblasts are absent.

The margins of adult leaves of the majority of *Tambourissa* species are entire and plane to revolute. Exceptional are *T. thouvenotii*, *T. trichophylla*, and the two species formerly included in *Phanerogonocarpus*, i.e., *T. alaticarpa* and *T. longicarpa*. The former two possess half-toothed leaves with one to eight pairs of Monimiod teeth in the apical portion of the lamina. In *T. trichophylla* (Fig. 7C), the secondary arches are strong and delimit low, broad intercostal areas, with an excurrency of the secondary arch running into each tooth. The apical portion of the lamina is therefore semicraspedodromous. In *T. thouvenotii* (Fig. 7A), the secondaries delimit high, narrow intercostal areas and the arches are much weaker, approaching the semicraspedodromous pattern of *Ehippiandra*. In some leaves of *T. thouvenotii* the main, apical secondary branch runs directly into the tooth, and any festooning is very weak. In others, it more closely resembles the pattern in *T. trichophylla*.

Leaves of the two species formerly included in *Phanerogonocarpus* (*T. alaticarpa* and *T. lon-*

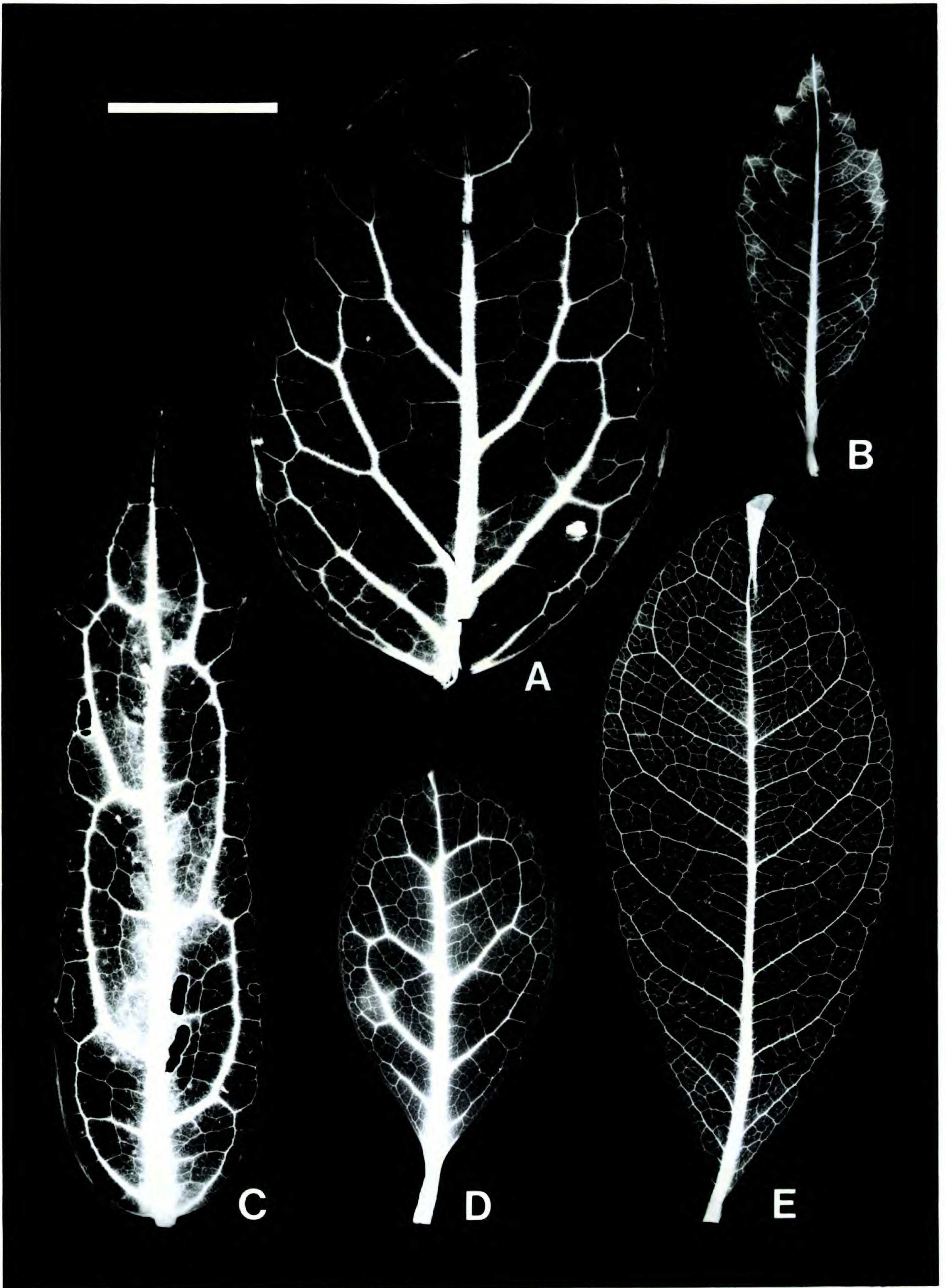


FIGURE 7. Leaf clearings of *Tambourissa*.—A. *T. thouvenotii*, Thouvenot s.n. in 1919 (BM).—B. *T. ficus*, juvenile from sucker shoot, Richardson 4042 (K).—C. *T. trichophylla*, Lorence 1879 (MO).—D. *T. elliptica* subsp. *elliptica*, Friedmann 2299 (P).—E. *T. elliptica* subsp. *micrantha*, Coode 4956 (K). Bar equals 25 mm.

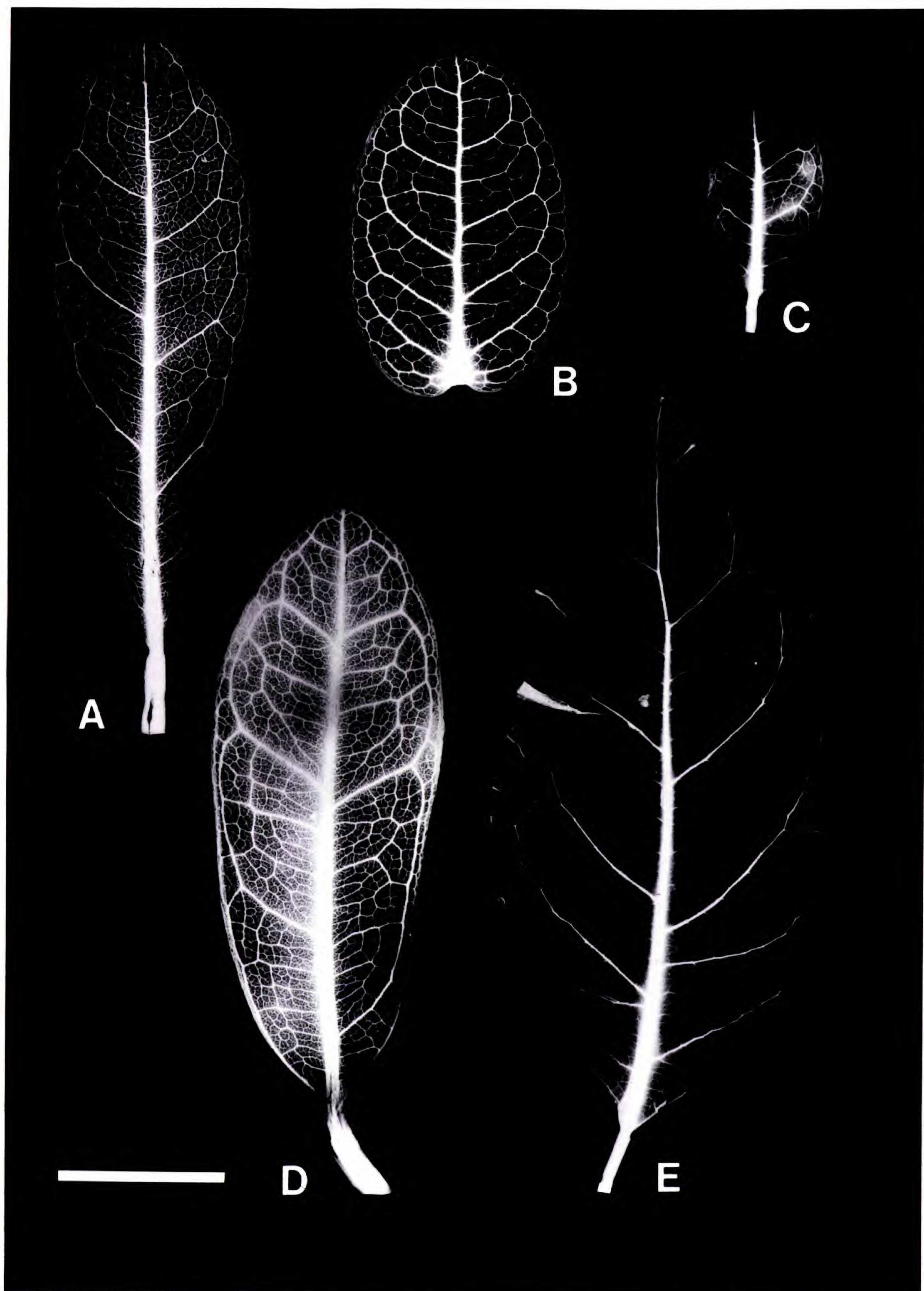


FIGURE 8. Leaf clearings of *Tambourissa*.—A. *T. peltata*, Guého sub MAU 12543 (MAU).—B. *T. cordifolia*, Lorence M 144 (MO).—C. *T. parvifolia*, Baron 4204 (K).—D. *T. religiosa*, Decary 6554 (P).—E. *T. leptophylla*, Tattersall s.n. (MO). Bar equals 25 mm.

gicarpa) have five to eight pairs of secondary veins arising at quite uniform angles which delimit fairly regular intercostal areas and unite in a festooned brochidodromous pattern. In *T. alaticarpa*, the apical $\frac{2}{3}$ – $\frac{3}{4}$ of the margin is dentate with eight to ten pairs of slender, antrorse teeth (Fig. 17A). That of *T. longicarpa* is broadly dentate with two or three pairs of large teeth in the apical $\frac{1}{3}$ – $\frac{1}{2}$ of the lamina. In both, the teeth arise from exmedial branches of the secondary or tertiary arches, thus rendering the venation semicraspedodromous.

In the context of Rury and Dickison's (1977) findings for *Hibbertia* where teeth develop in the adult leaves, it would seem that the dentate species of *Tambourissa* are advanced within the genus. My field studies show, however, that seedlings of virtually all species of *Tambourissa*, which I have seen, produce apically dentate leaves. This condition frequently also occurs on sucker shoots (e.g., *T. ficus*, Fig. 7B) where they are gradually lost in the ontogenetic transition to entire adult leaves. These *Tambourissa* species therefore appear to lose their teeth secondarily, as also occurs in *Hortonia* (Endress, 1980a). In this context, the four dentate species may represent cases of neoteny. This does not, however, contradict Hickey and Wolfe's (1975) suggestion that the Monimoid tooth is an advanced feature within the family.

TRICHOMES

Apart from the three virtually glabrous *Tambourissa* species mentioned above, stems and leaves of most species in all four genera bear at least some trichomes. Leaf pubescence ranges from a few scattered hairs along the petiole and major veins, to the entire lamina being canescent or velutinous-tomentose. Stem pubescence is comparable to that of the leaf. Trichomes of all the genera examined are nonglandular, lignified (e.g., stain pink or red with phloroglucinol; Hobein, 1889), and are simple and unicellular (except in *Monimia*). In a few *Tambourissa* species they are fasciculate, i.e., grouped into clusters of two or three.

Three types of trichomes occur in *Monimia*: long, unicellular; multicellular, fasciculate consisting of two to eight long, ascendent, unicellular arms united basally to form the stalk; short, appressed, multicellular stellate or stellate-peltate composed of six to 16 horizontal arms radiating from a common center and joined basally to form

the stalk. Trichome density is greatest on the abaxial laminar surface where they form a thick, whitish indument completely obscuring the leaf surface (Fig. 9E), whereas they are scattered and more easily distinguished on the adaxial surface. Trichomes play a key role in distinguishing the three species of *Monimia*. *Monimia ovalifolia* is distinct in having small, appressed, stellate-peltate trichomes with six to 16 short arms united basally for $\frac{1}{3}$ – $\frac{1}{2}$ their length (Fig. 9D, E), a character shared by populations both from Mauritius and Réunion. In addition to stellate trichomes with fewer long, free arms, *M. amplexicaulis* and *M. rotundifolia* also have simple and fasciculate trichomes (Fig. 9A–C). Although both the latter species may display considerable variation in trichome composition, even within a single population, they are modally distinct.

In the Mollinedioideae, *Ehippiandra domatiata*, *E. madagascariensis*, *E. microphylla*, *E. myrtoidea*, and *E. perrieri* are all sparsely pubescent or subglabrous with short, pale simple trichomes, whereas *E. tsaratanensis* is easily distinguished by its long, dense simple reddish trichomes. Trichomes of *Decarydendron* are simple, yellowish, and generally longer than in *Ehippiandra*. Leaf pubescence in *Tambourissa* ranges from completely glabrous in a few species (e.g., *T. cocottensis*, *T. tetragona*, species Group 5), to subglabrous (e.g., *T. tau*, species Group 5), canescent or villous in many (e.g., *T. nosybensis*, *T. hildebrandtii*, species Group 1B), or even densely velutinous-tomentose in a few (e.g., *T. thouvenotii*, *T. trichophylla*, species Group 1A; *T. longicarpa*, species Group 8). Trichomes therefore constitute a taxonomically useful character in the Monimiaceae.

INFLORESCENCE

Inflorescence structure in the four genera is quite variable: thyrsic, cymose (pleiochasial, dichasial, or monochasial), fasciculate, or solitary. Although more than one inflorescence type frequently occurs within a given species, and often on a single individual, the inflorescence generally provides a taxonomically useful suite of characters. Flowers of all the genera and species in this study are unisexual, and sexual makeup of the inflorescence is often stable and characteristic. For example, *Monimia* is invariably dioecious, although sex expression in the other taxa is often more variable. Inflorescence position varies greatly within the genera, but is frequently

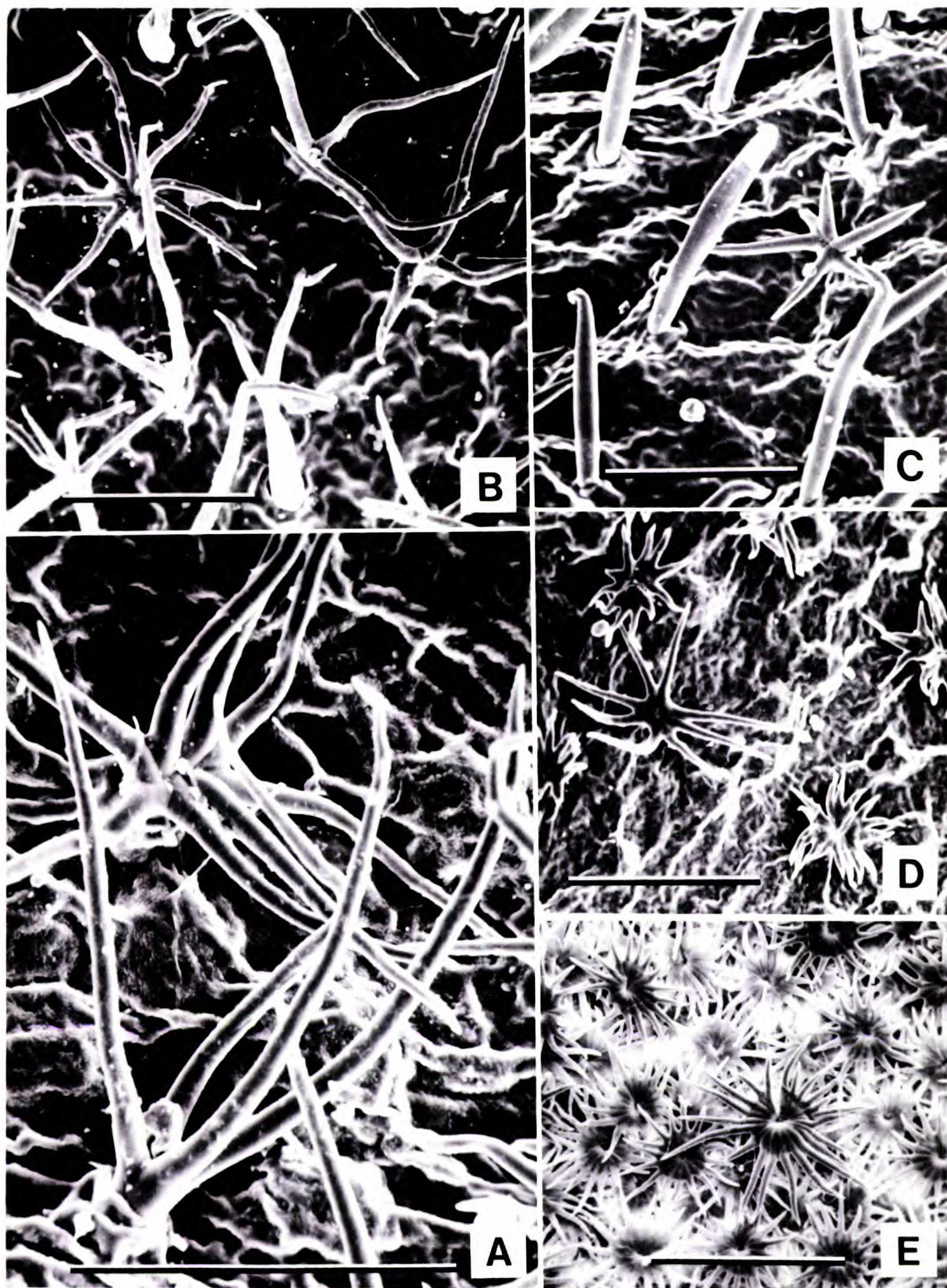


FIGURE 9. Scanning electron micrographs of *Monimia* leaf trichomes.—A. *M. amplexicaulis*, adaxial leaf surface, Capuron SF-28210 (P).—B. *M. rotundifolia*, adaxial leaf surface, Friedmann 781 (P).—C. *M. rotundifolia*, adaxial leaf surface, Bosser 21332 (P).—D. *M. ovalifolia*, adaxial leaf surface, Guého sub MAU 14097 (MAU).—E. *M. ovalifolia*, abaxial leaf surface, Friedmann 1884 (P). Bars equal 0.5 mm.

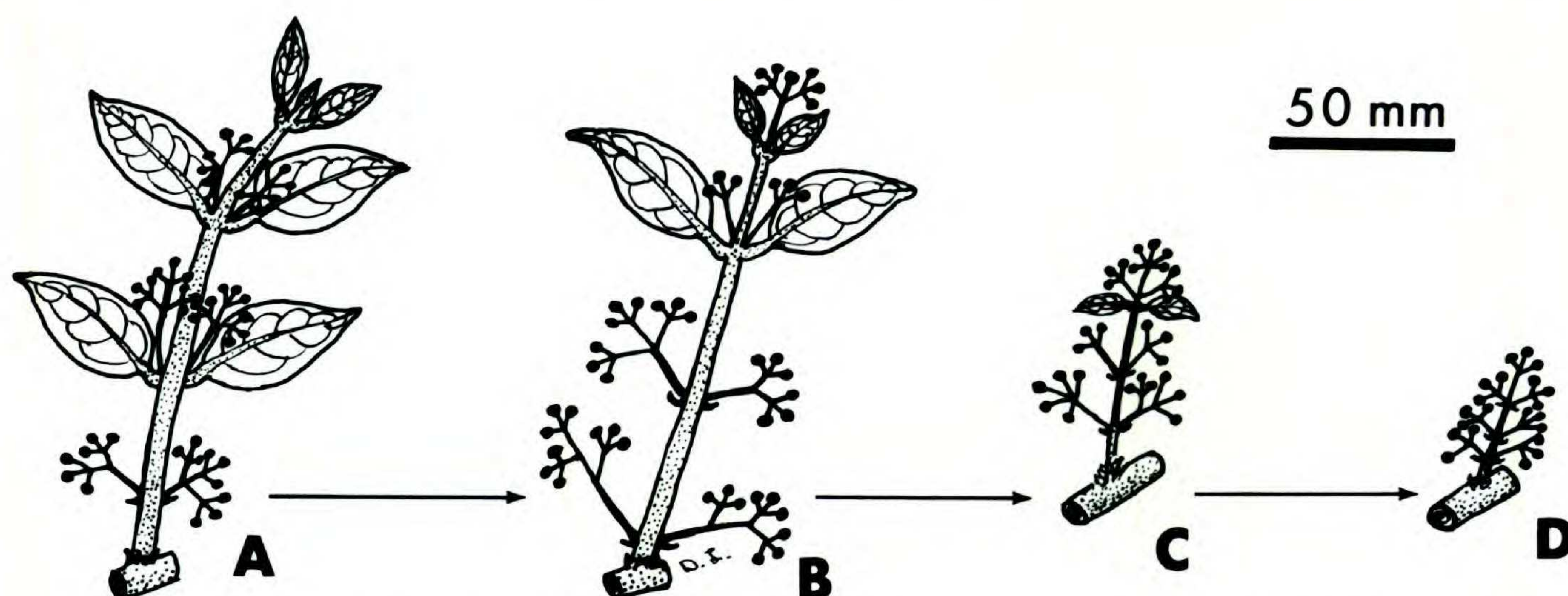


FIGURE 10. *Monimia* inflorescence types, hypothetical reduction series showing derivation of different types. Flowers are depicted as being in one plane, whereas they are actually decussately arranged.—A. Indeterminate leafy shoot with axillary thyrse.—B, C. Determinate leafy thyrse.—D. Thyrse. Bar equals ca. 50 mm.

modally distinct for given species. A brief review of the inflorescence characters will be given for each genus.

Observations on numerous herbarium specimens and living plants reveal that all three species of *Monimia* are dioecious. Inflorescences of all three species are extremely polymorphic and have been variously described as panicles, umbels, racemes (e.g., Baker, 1877), and cymes (Hutchinson, 1964). The ultimate determinate floral unit consists of from two to eight, but usually three, flowers on subequal pedicels attached to a common axis at the same point. As all the flowers in the unit are of the same sex and size, and furthermore all open at about the same time, it does not represent a cyme or pleiochasium in the usual sense (e.g., Lawrence, 1951), but is truly umbelloid. Groups of two to four umbelloid units may be further aggregated or dispersed along a common axis in a thyrse-like manner. The resulting units are borne decussately on a central axis in various ways; up to four different inflorescence types may occur on a given individual, all ramiflorous. These appear to represent a reduction series from an indeterminate leafy shoot with simple axillary thyrse to a leafless, determinate thyrse (Fig. 10A–D).

A) The discrete umbelloid or thyrseic floral units are axillary and occasionally subfoliar on leafless nodes near the basal portion of the actively growing, indeterminate leafy shoot. Each subfoliar unit is subtended by a single caducous, brown bract presumably representing a reduced leaf.

B) The next stage involves the addition of a terminal floral unit. Addition of further lateral

units with a concomitant reduction in the number of leaves, which are replaced by bracts, results in the entire structure becoming a determinate leafy thyrse.

C) Further suppression of leaves and shortening of the floral axis results in a more contracted, but still leafy, thyrse.

D) Finally, suppression of all the leaves and their replacement by bracts and still further shortening of the floral axis results in a true thyrse. A similar reduction series occurs in *Tambourissa*, ultimately resulting in a monochasium.

In *Monimia ovalifolia*, the ultimate floral units are generally quite contracted, although the secondary axes may be elongated, with up to 87 flowers per inflorescence. The inflorescence of *M. amplexicaulis* is invariably short and contracted, consisting of not more than 37 flowers in specimens I have examined. Inflorescence structure is much more variable in *M. rotundifolia*, ranging from short and contracted to lax and elongated with up to 76 flowers. Plants of the latter type were described as *M. citrina* by Tulasne. Such variation may occur within a single population, e.g., at Col de Bellevue, Réunion (Lorence 2471–2474; 2773–2775, all MO). In view of the variability of inflorescence structure in *Monimia*, it is not a particularly useful taxonomic character.

The basic inflorescence unit in the three species of *Decarydendron* (all monoecious) is a sexually mixed or unisexual pleiochasium (termed “spiciform” by Danguy, 1928). It consists of an elongated floral axis bearing two to four decussate or subalternate pairs of pedicellate androecious

THE AMPHIBIA OF GREER COUNTY, OKLAHOMA¹

ARTHUR N. BRAGG²

Greer County, Oklahoma, lies not quite in the southwestern corner of the state. It is bounded on the north by Beckham, on the east by Kiowa, on the south by Jackson, and on the west by Harmon counties. It is drained by three major streams: (1) the North Fork of the Red River which separates it from Kiowa County all along its eastern edge, (2) the Elm Fork which cuts diagonally southeastward through its center to enter the North Fork, and (3) the Salt Fork of the Red River which flows eastward and then southward in the southern portions of the county.

Greer is essentially one of the prairie counties of Oklahoma. Probably originally mixed grassland is it now largely short grass prairie. However, in its western and northwestern portions considerable areas of gypsum rock come to the surface and this in some places has caused a rugged relief and a change in vegetation locally as differential erosion has occurred. Similarly, along its eastern border, great granitic masses known as the Granite Mountains occur as largely bare and steep rock up-thrusts from the surrounding plain. These are the western outliers of the Wichita Mountains. In many places in the grassland areas, especially in flat lands along small creeks, smaller or largest stands of mesquite dominate or partially dominate the landscape. Some such stands of mesquite savannah are very extensive like the one in which I once lost my direction and floundered around for an hour or more before wandering onto a section line road running through it and thus finding my way out.

This area of Oklahoma has deficient rainfall, high winds, and high temperatures. The evaporation rate from all water surfaces is very rapid, especially during summer. Fast development is a necessity for any amphibian here that uses temporary pools for breeding, as most of them do. Only one salamander occurs in this region so far as known and no others are expected. The remainder of the Amphibia are Salientia.

1. *Ambystoma tigrinum morvortium* Baird

This "prairie edition" of the tiger salamander is very abundant in all parts of the county. It is a nocturnal, burrowing form whose adults are rarely seen except after rains. Spring and summer rains apparently stimulate breeding—at least, the adults enter the water for breeding at such times only, so far as I can determine. They breed in temporary water (ditches particularly) farther north in western Oklahoma but in Greer County I have found their larvae only in the cattle tanks, some of which here are quite deep (6-12 feet or more) when full. In deep tanks, the larvae will be found only in the deeper (and therefore cooler) water on very hot days.

1. Contribution of the Department of Zoology and of the Biological Survey, University of Oklahoma, Norman.

2. Professor of Zoology and Herpetologist of the Biological Survey, University of Oklahoma.

In tanks in the gypsum regions, the larvae are very light colored, light cream all over except the tail tip which is intensely black and the gill bars which are bright golden. In waters off the gypsum they are a nondescript greenish-brown; lighter in turbid than in clear water, but never like those on the gypsum.

If one traverse the whole county in June, sampling many tanks, he is struck by the different sized larvae commonly found. In one tank they may be tiny, in another half grown, in still a third intermediate in size. However, within any one region adjacent tanks tend to have larvae of comparable sizes and in a single tank it is rare to find more than two size groups, - usually only one. This phenomenon is associated with rainfall pattern and reflects the dependency of breeding adults upon rainfall for their breeding activities. This is more striking in some years than in others, of course, but so clear cut that during most years one could, by sampling pools for larval sizes, draw a fairly accurate pattern of the rainfall over the county a month or two before. In some years larvae are rare; in others, abundant.

I have not seen their metamorphosis in this region. It sometimes, at least, occurs in July in some other parts of western Oklahoma, north of Greer County.

2. *Acris crepitans* Baird.

Common on muddy banks of pools everywhere, breeding in the adjacent waters. Calling begins usually in April and is intermitant all summer. Most breeding is after the spring rains.

3. *Bufo cognatus* Say.

Very abundant breeding after rains only, in temporary pools.

4. *Bufo compactilis speciosus* Baird.

This is the most abundant toad in this region, breeding after rains in temporary pools, but also in the edges of cattle tanks and in pools along the rivers. This toad and *Bufo cognatus* occur together in all parts of the country. *Bufo compactilis speciosus* tends to be the more abundant on the higher land between stream valleys.

5. *Bufo debelis debelis* Girard.

Following the nomenclature of Sanders and Smith (1951), this is the form to be found here. It is present throughout the county but in small numbers only. It is most abundant on mesquite flats and is unknown immediately near the larger streams. Like the other prairie toads it breeds after rains only and in temporary pools. It must have a very rapid development to exist using so shallow water. That it does so is evidenced also by my consistent misjudging when to return to the site of a breeding congress in an attempt to get its tadpoles, which, until recently, I have been unable to see. I have never seen its eggs which are still undescribed.

6. *Bufo punctatus* Baird and Girard.

This little toad of the rocky and rough regions of Oklahoma is known in Greer County from only one specimen collected in early morning after a rain in the night at the foot of one of the Granite

Mountains. Since it occurs in the prairies in Beckham County to the north (Bragg and Dundee, 1950) and is generally found in gypsum country in western Oklahoma, it presumably occurs sparingly over much of Greer County.

7. *Bufo woodhousei woodhousei* Girard.

This is the abundant toad of lawns and gardens and under streetlights in towns in Greer County. It is also the dominant toad along the streams but it occurs also in prairies and mesquite flats. It is, however, rarer on the higher areas between the streams. It breeds in both temporary and permanent waters and, whereas rain greatly stimulates its breeding, it is not a necessity to it. Mixed breeding congresses of this toad with *Bufo cognatus*, *Bufo compactilis speciosus*, and *Bufo debelis debelis* and members of other genera are the rule rather than the exception after rains in spring and early summer.

8. *Microphyla caroliensis olivacea* (Hallowell).

Abundant everywhere, breeding in rain-formed pools, immediately after rains from late April on through summer. Embryos and tadpoles have a very rapid development but this has not yet been accurately measured.

9. *Pseudacris clarki* Baird.

Very abundant in prairie, breeding in temporary, shallow, well-vegetated pools after rains.

10. *Pseudacris nigrita triseriata* (Wied). (?)

I once found tadpoles in a tank in Greer County which I identified at that time as of this form. Later I ran these down to this subspecies in testing a key (Bragg, 1950) then in preparation. However, I doubt my own record now on ecological grounds and recommend waiting until someone succeeds in finding adults here before definitely placing them in the list of Greer County forms.

11. *Rana catesbeiana* Shaw.

Very common in the larger tanks.

12. *Rana pipiens berlandieri* Baird.

13. *Rana pipiens brachycephala* Cope.

Leopard frogs are very abundant about water everywhere. Some are certainly *R. p. brachycephala*. Further observations are needed in these frogs here as well as elsewhere.

14. *Scaphiopus couchi* Baird.

The southern spadefoot is very abundant in all parts of Greer County. It is common on the roads on summer nights and is sometimes found under streetlights with *Bufo*. It breeds after rains in shallow temporary pools. The exact time relations of its tadpole stages are not known, but I have many indications that the development is very rapid. I have several times failed to find tadpoles two and a half to three weeks after a known breeding congress had produced eggs.

15. *Scaphiopus bombifrons* Cope.

16. *S. hammondi* Baird.

The former of these two is abundant in all parts of Greer County but the latter is rather questionably present. I reported it from tadpoles collected in the gypsum region of the northwestern part of the county (Bragg, 1948), recognizing its tadpoles by the characteristic mouth parts (Smith, 1934; Bragg, 1941). However, Stebbins (1951) has cast doubt on the validity of the beak-notch relationship of the mandibles, having found many intermediate conditions in the western United States. I can confirm him in his facts. In western Oklahoma, including Greer County as well as several others, tadpoles with various intermediate conditions of beak-notch relation have been found. I have known such specimens from the Oklahoma Panhandle for at least twelve years. However, I have always found such specimens within the habitat of *S. bombifrons* when *S. hammondi* were also present: where *S. bombifrons* occurs alone, as in central Oklahoma, none have ever been found with any marked degree of the beak-notch character. Accordingly, I have interpreted the facts to indicate interbreeding between these two in areas where *S. hammondi* is present in small numbers only, the bulk of the population as in Greer County being *S. bombifrons* (Bragg, 1946). The fact that some of the tadpoles studied to the west of Oklahoma may have come from regions where *S. bombifrons* does not occur gives considerable weight to the interpretation of Stebbins as opposed to my own. I do not think the problem settled, however. More observations are needed.

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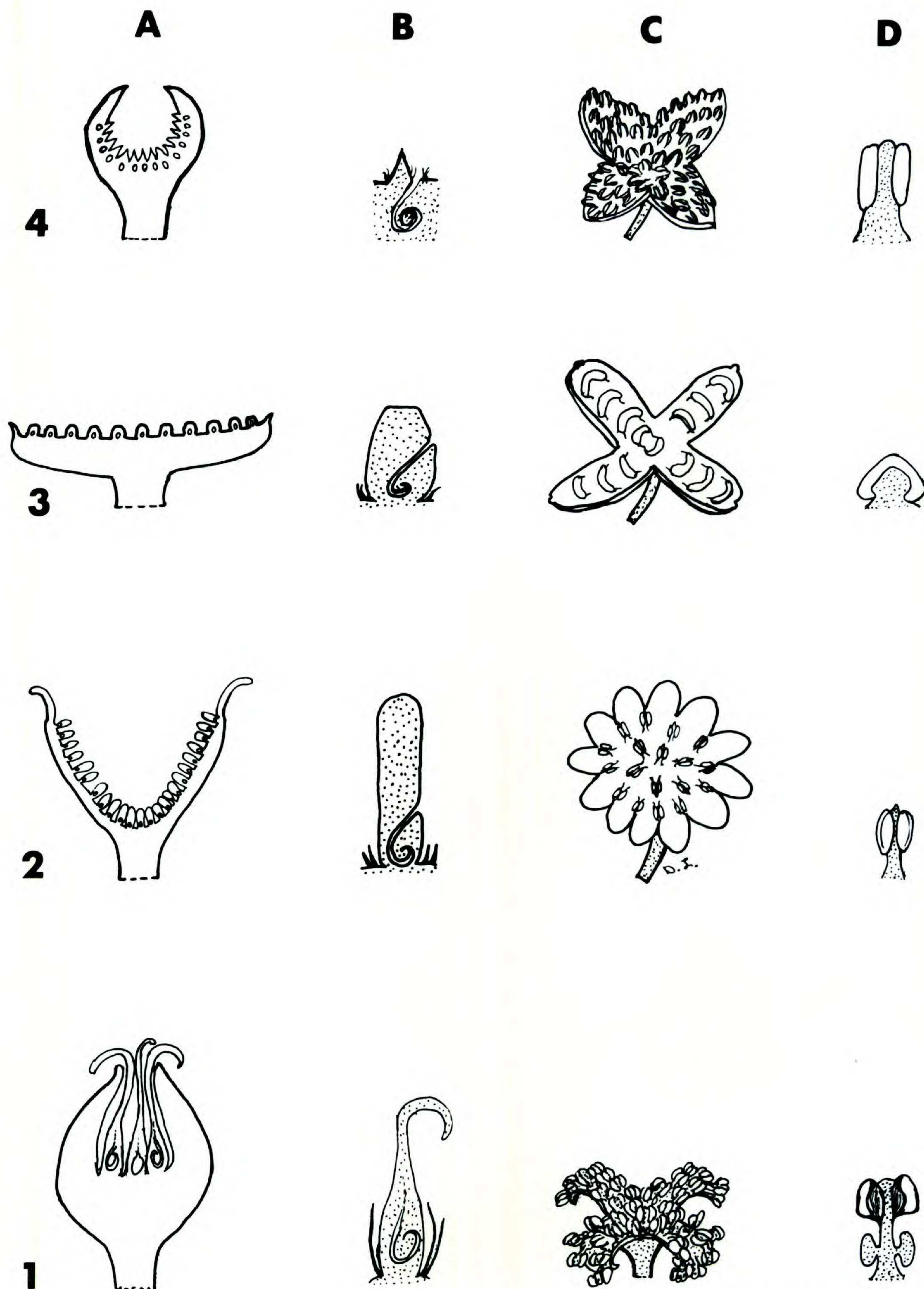
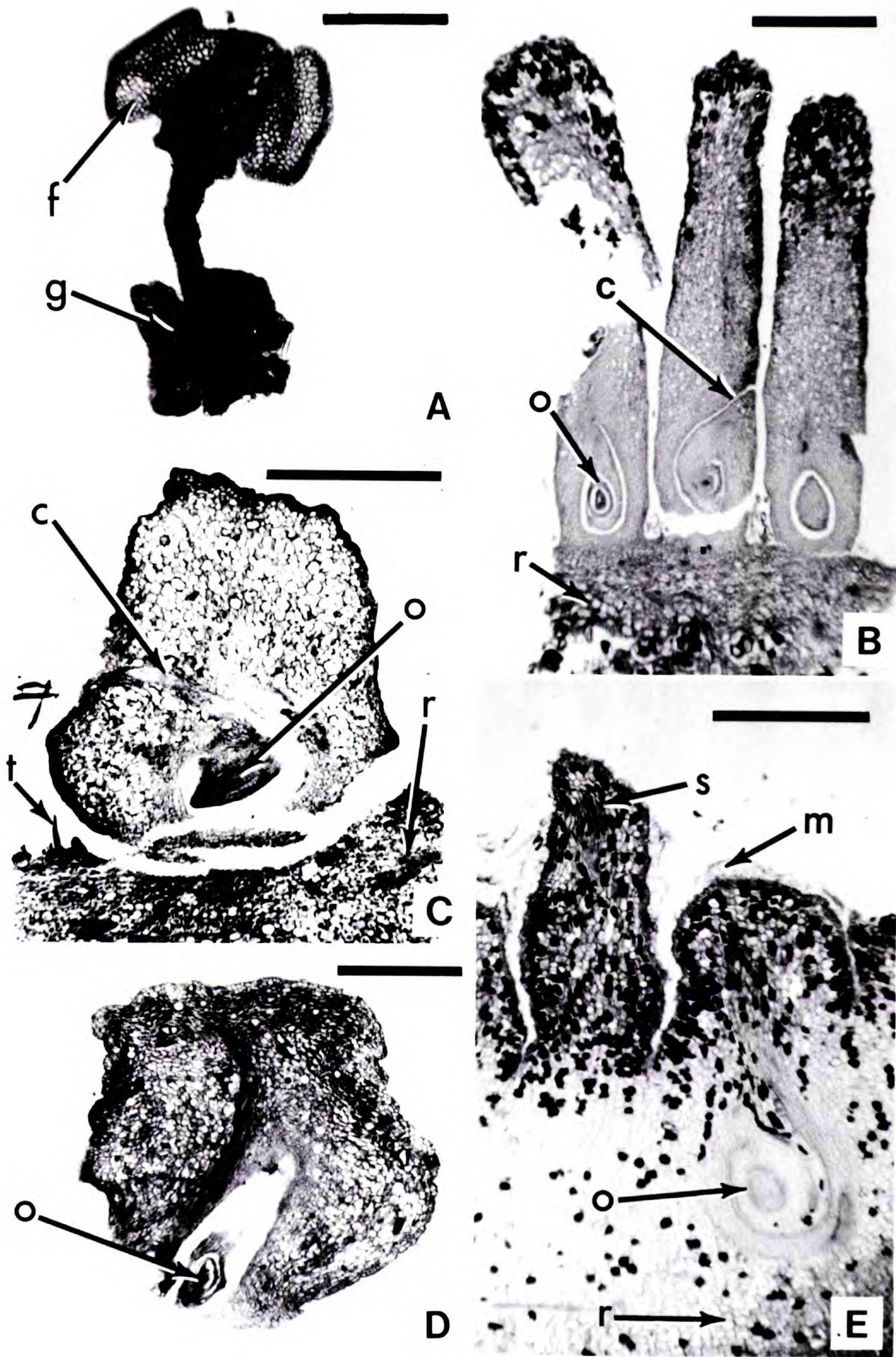


FIGURE 12. Schematic drawings of flowers of the four genera of Monimiaceae in the Malagasy region. 1. *Monimia*; 2. *Decarydendron*; 3. *Ehippiandra*; 4. *Tambourissa*.—A. Gynoecious flower, longitudinal section.—B. Individual carpel, longitudinal section.—C. Androecious flower at anthesis.—D. Stamen. Not to scale.



whorled series. The tepals are infolded in bud and the flowers consequently do not split, but open gradually at anthesis as the tepals become erect or everted. The external receptacle surface is often pubescent with simple trichomes.

At anthesis the gynoecious flower of *Decarydendron* is hemispherical or obconical with thick walls and straight or slightly incurved tepals. Numerous free, clavate carpels line the inner receptacle surface (ca. 300 in *D. helenae*) and are interspersed with short, densely tufted simple lignified trichomes. In *D. helenae* var. *stenophyllum* (Humbert 6613, K), each carpel is clavate or cylindrical, ca. 1.5 mm long, slightly constricted basally and obtuse apically (Fig. 13B). A single, pendulous anatropous bitegmic ovule is contained in a small loculus which is confined to the base of the carpel and from which the oblique styler canal runs upward and opens at the side of the carpel in its basal third (Fig. 13B). The carpellary ground tissue contains scattered oil cells above the ovary and densely aggregated stone cells in the terminal portion (Fig. 13B). Stone cells also occur in the receptacular ground tissue, but no tanniferous idioblasts were observed. In cleared carpels, a single vascular bundle enters from the base, supplies the ovule, and extends upward almost to the apex, terminating in tracheoids. The exterior surface of the carpel is possibly secretory in nature as in many Monimiaceae (Endress, 1980b), but no traces of mucilage were observed.

In the androecious flower, from 16 to 60 stamens are irregularly dispersed over the glabrous to pubescent inner surface of the shallowly concave or cupuliform receptacle (Figs. 12.2C, 14E). Stamens of all three species are comparatively unspecialized with a distinct, narrow filament, unprolonged connective, and separate, laterally dehiscent, tetrasporangiate anthers (Fig. 12.2D).

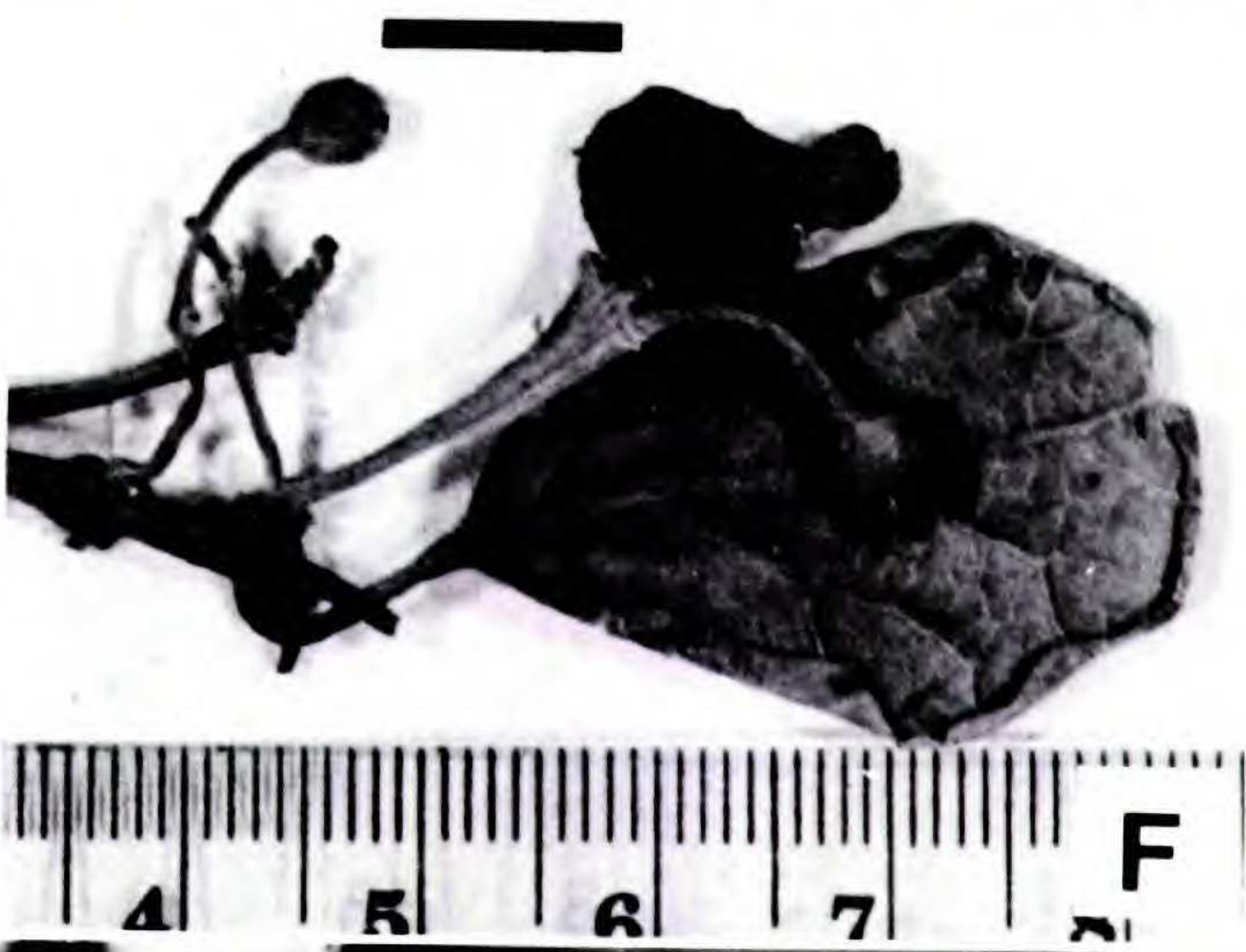
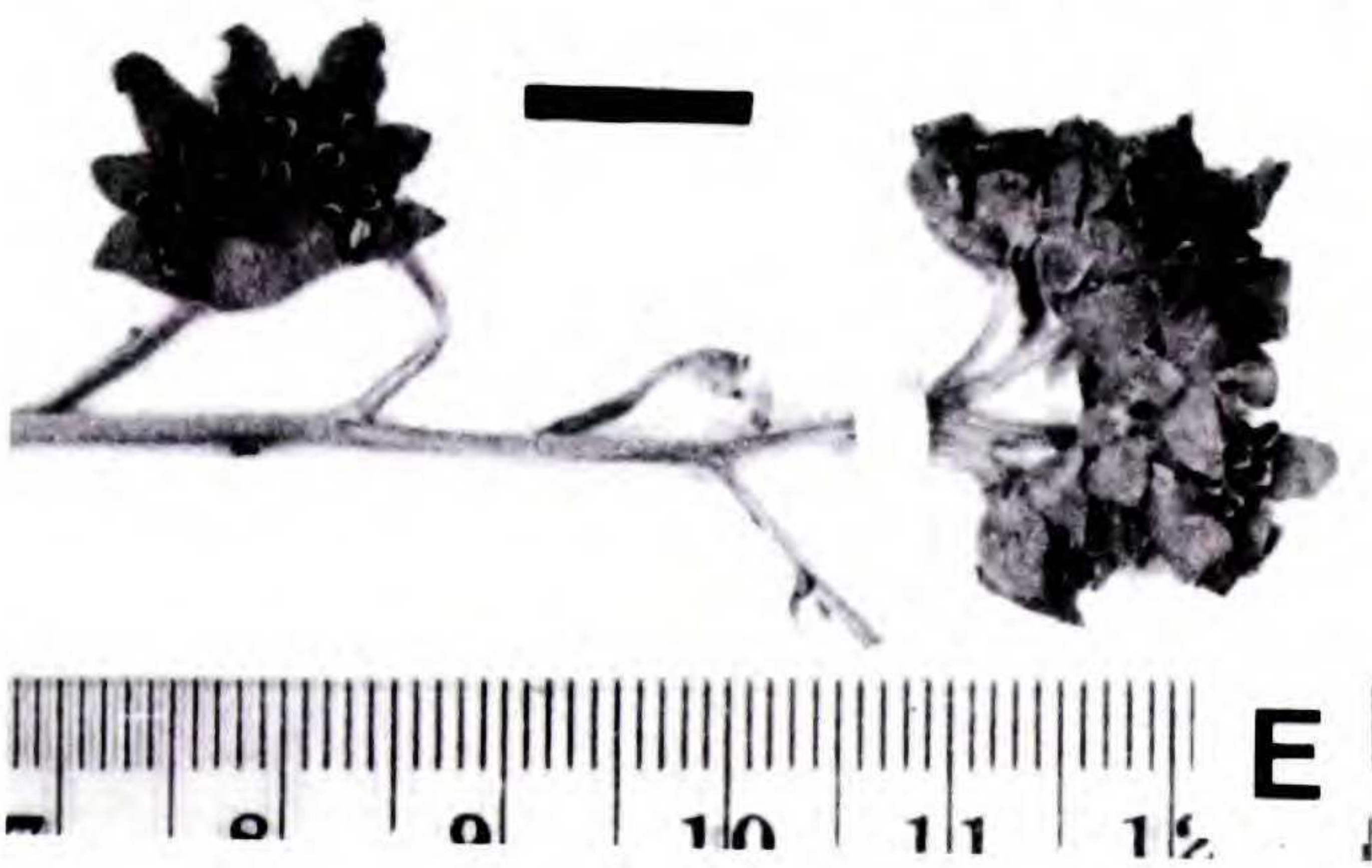
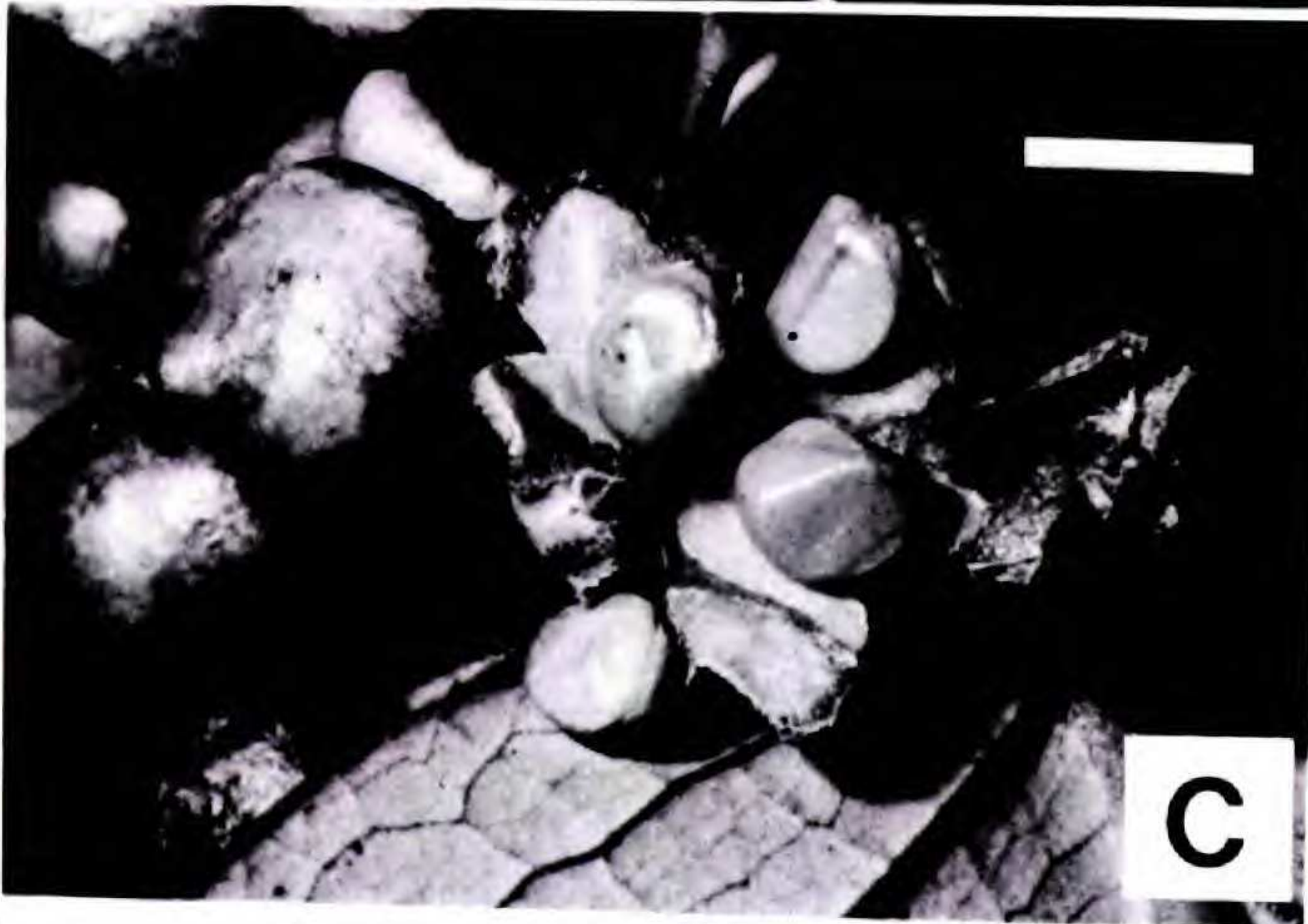
Useful taxonomic features of *Decarydendron* flowers include: number and size of tepals and characters of their margins (crenulate or not); number of stamens; size of the receptacle and presence or absence of lateral ridges (Cavaco,

1959). The genus is clearly the least specialized florally of the Mollinedioideae in the Malagasy region.

Floral construction in *Ehippiandra* (including *Hedycaryopsis*) is more specialized, including a strong male/female floral dimorphism (Figs. 12.3A–D, 14F, G). Gynoecious flowers are somewhat globular and concave in bud, but open gradually and become discoid during ontogenetic development. In *Ehippiandra madagascariensis* (Bernardi 11977, K, MO), the receptacular rim initially bears four small, decussate, deltoid tepals which apparently divide once by lateral doubling, resulting in eight tepals in the mature flower. Most species also appear to have four, eight, or rarely 16 minute, decussate tepals, and the receptacles are externally pubescent with short to long simple hairs. At anthesis the receptacle is flat and discoid, crowded with 20–150 free, sessile, shortly columnar carpels interspersed with clusters of simple, lignified trichomes (Fig. 12.3A, B). Each carpel is four to six sided, ca. 1–1.5 mm long, with a flat top, straight to inclined sides, and a slightly constricted base (Fig. 13C, D). The solitary ovule is anatropous or amphitropous and bitegmic, situated in a small loculus near the base of the carpel, with a styler canal leading obliquely upward and opening at the side near the middle of the carpel (Fig. 13C, D). The entire carpel is covered by an epidermal layer which appears to be secretory and produce mucilage at least around a central zone. Occasional short, simple hairs occur on the carpellary surface in *E. madagascariensis*. In cleared carpels, two vascular bundles enter from the base on either side of the ovule in *E. myrtoidea*, *E. madagascariensis*, and *E. tsaratanensis*, and fan out into a zone with numerous, terminal tracheoids near the apex. Endress (1980a) also found tracheoids in other genera and suggested that they might function as water storage cells. The ventral bundle gives rise to a weak, arcuate secondary branch supplying the ovule. The floral ground tissue of *E. myrtoidea* contains oil cells, stone cells, and large numbers of tanniferous idioblasts. That of *E.*

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FIGURE 13. Photomicrographs of floral parts.—A. Stamen of *Monimia amplexicaulis* showing nearly introrse dehiscence and basal glands, whole mount, Lorence 2444 (MO).—B. Carpels of *Decarydendron helenae* var. *stenophyllum*, longitudinal section, Humbert 6613 (K).—C. Carpel of *Ehippiandra madagascariensis*, longitudinal section, Bernardi 11977 (MO).—D. Carpel of *E. myrtoidea*, longitudinal section, Parker s.n. (K).—E. Carpel of *Tambourissa cordifolia*, longitudinal section, Lorence 2630 (MO). Bars equal 0.5 mm. c = canal leading to ovule; f = flap of anther loculus; g = glands at base of stamen; m = mucilaginous exudate; o = ovule; r = receptacular ground tissue; s = style; t = trichome.



tsaratanensis contains both oil cells and numerous tanniferous cells, whereas only oil cells occur in *E. madagascariensis*. Receptacular ground tissue of these three species contains idioblasts comparable to those found in the carpels. The fewer and shorter, sessile carpels and reduced, decussate tepals of *Ehippiandra* represent specializations in comparison with *Decarydendron*.

Androecious flowers of *Ehippiandra* are globular and closed in bud (Fig. 14F, G), externally pubescent with short to long simple hairs, and generally bear four pairs of small to minute, acute to deltoid, decussate tepals at or near the apex (Fig. 12.3C, D). At anthesis, the floral cup splits by lateral fissures into four subequal, valvate segments exposing the 9–50 stamens (Fig. 12.3C, D) scattered or situated in several series on the glabrous to pubescent inner receptacle surface. The apex of each lobe usually bears one or rarely two obtuse, scale-like tepals in all but *E. myrtoidea*. The tetrasporangiate stamens range from ligulate and incurved to short, broad, and obtusely deltoid. Those of *E. domatiata*, *E. madagascariensis*, *E. perrieri*, and *E. tsaratanensis* are somewhat longer with more distinct filaments, separate loculi, and slightly prolonged or apiculate connectives, whereas those of *E. microphylla* and *E. myrtoidea* are generally shorter and sessile or subsessile with the loculi apically connivent or confluent into a single, crescentiform loculus. Staminal types within the genus intergrade, however, and a comparable range of variation occurs in *Tambourissa*. Dehiscence is lateral and longitudinal, but is continuous in stamens with a single, crescentiform loculus (both separate and confluent loculi may occur in a single flower, e.g., *E. myrtoidea*). *Ehippiandra microphylla* and *E. myrtoidea* have few (10–18), highly reduced stamens with connivent or confluent loculi; these represent specialized features.

Taxonomically useful characters in *Ehippiandra* flowers include: size of the receptacle; number of carpels, stamens, or tepals; presence

or absence of tepals on the inner receptacle lobes; size and shape of tepals; size and shape of stamens; condition of the loculi (free or confluent). Floral reduction in the genus shows specialization over *Decarydendron*.

Floral construction in *Tambourissa* (including *Phanerogonocarpus*) displays a number of still more specialized trends, one being a strong androecious/gynoecious floral dimorphism (Fig. 12.4A–D), except in *T. pedicellata*, *T. purpurea*, and a few other species. Perhaps the most striking and important trend is apparent in the gynoecious flowers, which have their carpels immersed in and fused with the receptacular wall and are therefore inferior and syncarpous (Endress, 1979, 1980b), thus showing considerable advancement over *Decarydendron* and *Ehippiandra*. Although androecious flowers of some *Tambourissa* species are comparable to those of *Ehippiandra*, those of other species are even more specialized. Because a more detailed study of the ontogeny and floral construction of *Tambourissa* has been published elsewhere (Endress & Lorence, 1983), only a brief account is given here.

Gynoecious flowers of *Tambourissa* consist of a massively developed receptacle which is generally closed in bud. Considerable variation occurs in receptacle size and morphology, the main types of which are shown in Figure 15. The receptacle is more or less napiform or cup-like in the majority of species (e.g., *T. cordifolia*, *T. ficus*, *T. pedicellata*; Fig. 15B, C, J), but ranges from flat and discoid in *T. peltata* (Fig. 15A), to closed and spherical in *T. sieberi*, or even cylindrical in *T. alaticarpa* and *T. longicarpa* (Fig. 15E, H). Both the flat, open and the closed, globose or cylindrical types appear to be highly specialized and derived from a more generalized cupuliform type like that found in *T. pedicellata*. The receptacles of *T. alaticarpa* and *T. longicarpa*, although extremely elongated and laterally winged, still fall within the range of variation displayed by certain other species. For example,

FIGURE 14. Flowers and fruits. —A. *Monimia ovalifolia*, androecious inflorescence at anthesis, Lorence 2896 (MO). —B. *M. ovalifolia*, gynoecious inflorescence at anthesis, note exerted styles (s), Lorence 2757 (MO). —C. *M. ovalifolia*, ripe fruiting receptacles splitting to expose carpels, Coode 4954 (K). —D. As for C, Lorence 2350 (MO). —E. *Decarydendron lamii*, terminal portion of androecious inflorescence with expanded androecious flower showing stamens and large tepals, Lam & Meeuse 5835 (P). —F. *Ehippiandra madagascariensis*, inflorescences showing globose androecious flowers in bud and central discoid gynoecious flower, Ursch 66 (P). —G. *E. perrieri*, flowering stem showing globose androecious flowers in bud and discoid central gynoecious flower, Perrier de la Bâthie 16249 (P). —H. *E. tsaratanensis*, old infructescence with carpels gone (left), and submature infructescence with three green carpels seated in basal cupules (right), Gentry 11605 (MO). Bars equal 10 mm.

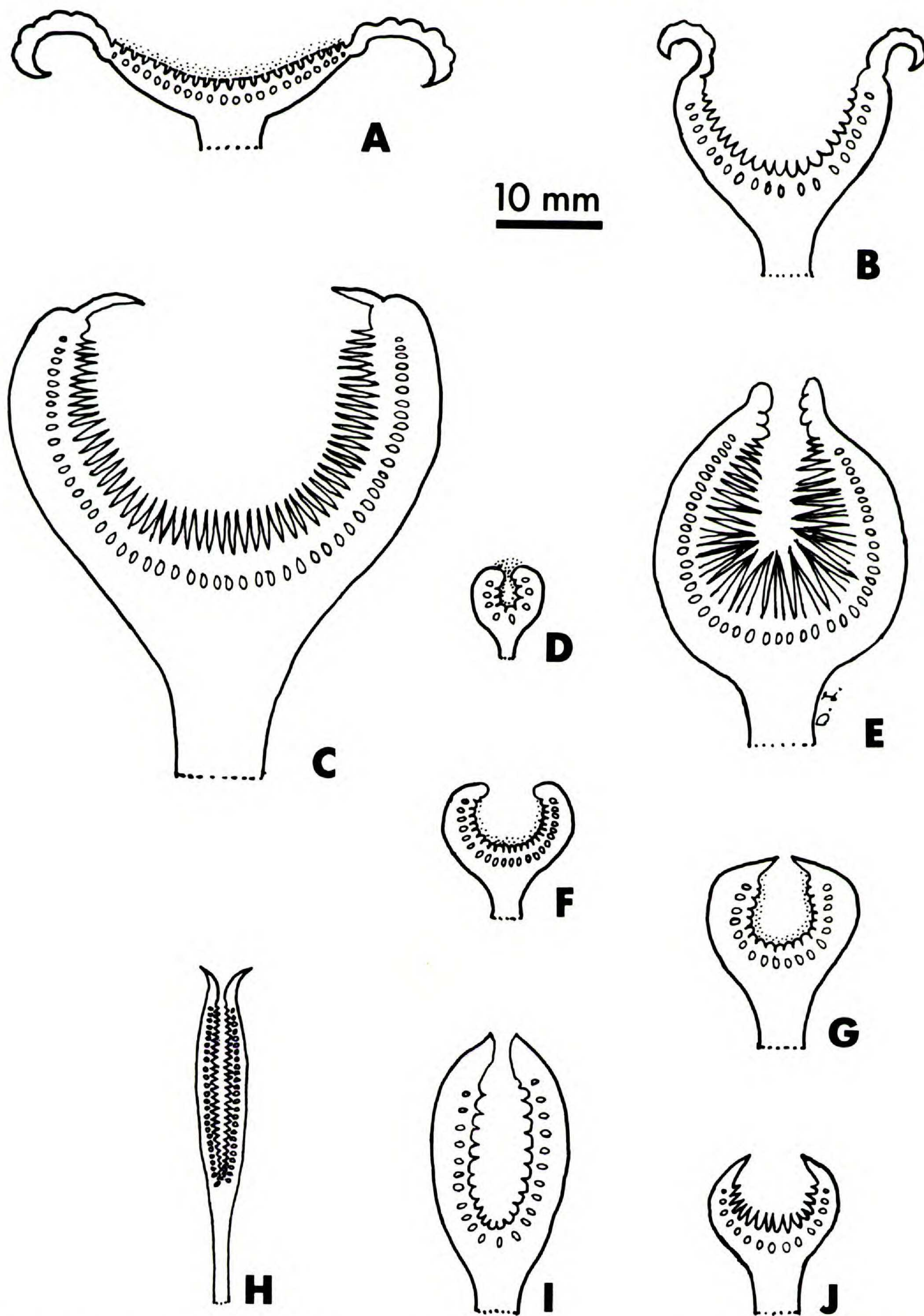


FIGURE 15. Schematic longitudinal sections through gynoecious floral receptacles of some *Tambourissa* species.—A. *T. peltata*.—B. *T. cordifolia*.—C. *T. ficus*.—D. *T. purpurea*.—E. *T. sieberi*.—F. *T. comorensis*.—G. *T. elliptica*.—H. *T. alaticarpa*.—I. *T. quadrifida*.—J. *T. pedicellata*. Stippled areas represent mucilaginous com-pitum. Drawn to approximate scale.

gynoecious receptacles of *T. quadrifida* are cylindrical-ellipsoid, and those of *T. floricostrata* bear four lateral, longitudinal ridges. The external receptacular surface in the genus ranges from glabrous (e.g., *T. tetragona*) to densely velutinous (e.g., *T. sieberi*) or corky (e.g., *T. tau*).

The gynoecious bud apex in *Tambourissa* generally bears several pairs of minute, decussate obtuse or deltoid, scale-like tepals. Two pairs are usually visible externally in most species, and these are sometimes fused into an apicule (e.g., in *T. sieberi*, *T. tau*). In *T. purpurea* there are usually five pairs; the innermost are enclosed in the floral cup and intergrade into the carpels (Endress, 1980b; as *T. religiosa*). In several of the Comorean species in Group 2 (*T. comorensis*, Figs. 15F, 17B; *T. kirkii*; and *T. leptophylla*) where the gynoecious receptacle remains open during the entire floral development, the tepals are apparent only during the very young stages. This is an unusual feature within the genus, and could represent either a highly advanced character or, alternatively, a transitional stage between the open, discoid receptacles of *Ehippiandra* and the closed buds of most *Tambourissa* species. At floral anthesis, the receptacles of most species generally split open by shallow (e.g., *T. purpurea*) to deep (e.g., *T. peltata*) longitudinal fissures between the tepals, forming a number of subequal lobes ranging from four in most species (e.g., *T. cordifolia*, Fig. 42G, H) to as many as eight or ten in *T. ficus* (Fig. 15C) and *T. tau* (Fig. 39E). The sterile internal surface of the lobes may be pubescent (e.g., *T. moheliensis*, Fig. 36E) or glabrous (*T. tau*). Inner lobes of *T. peltata*, and to a lesser degree *T. cordifolia*, are sculptured with longitudinal ridges or lines, somewhat verrucose in the former species and bearing stomata in both species (Endress & Lorence, 1983). Position of the lobes at anthesis ranges from incurved (e.g., *T. pedicellata*, Fig. 15J), or erect (e.g., *T. hildebrandtii*), to spreading-reflexed (e.g., *T. peltata*; Figs. 15A, 17E). The colorful, everted lobes of *T. peltata* have assumed the function of the perianth.

The carpels of *Tambourissa* are immersed in and united with the receptacle wall and are therefore inferior and syncarpous in a morphological sense (Endress, 1979, 1980b, 1982), not embedded in sockets as stated by Baillon (1871) and Corner (1976). Each carpel is unilocular with a solitary, bitegmic, anatropous ovule (amphitropous in *T. decaryana*, *T. nosybensis*). The two species formerly included in *Phanerogonocarpus*

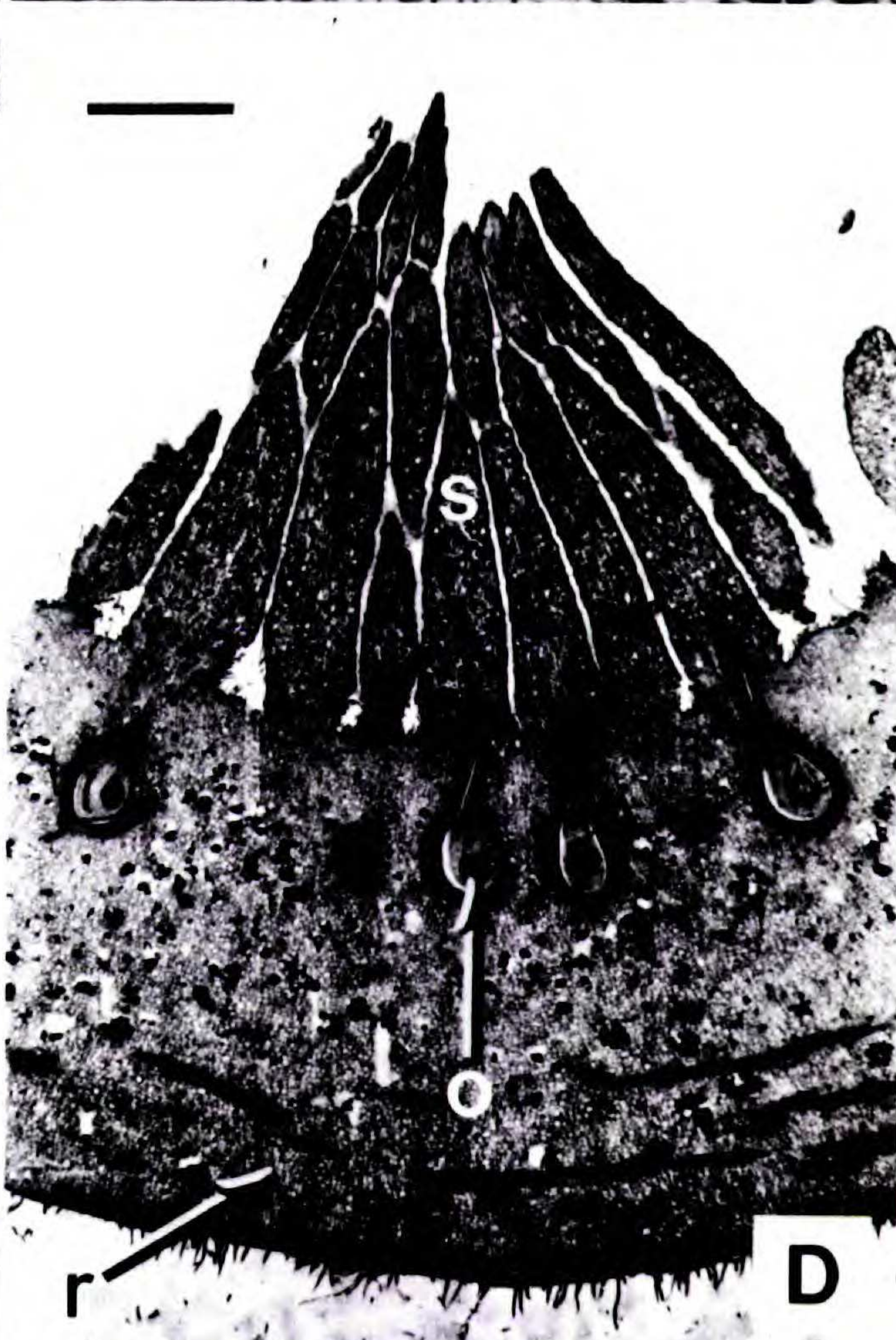
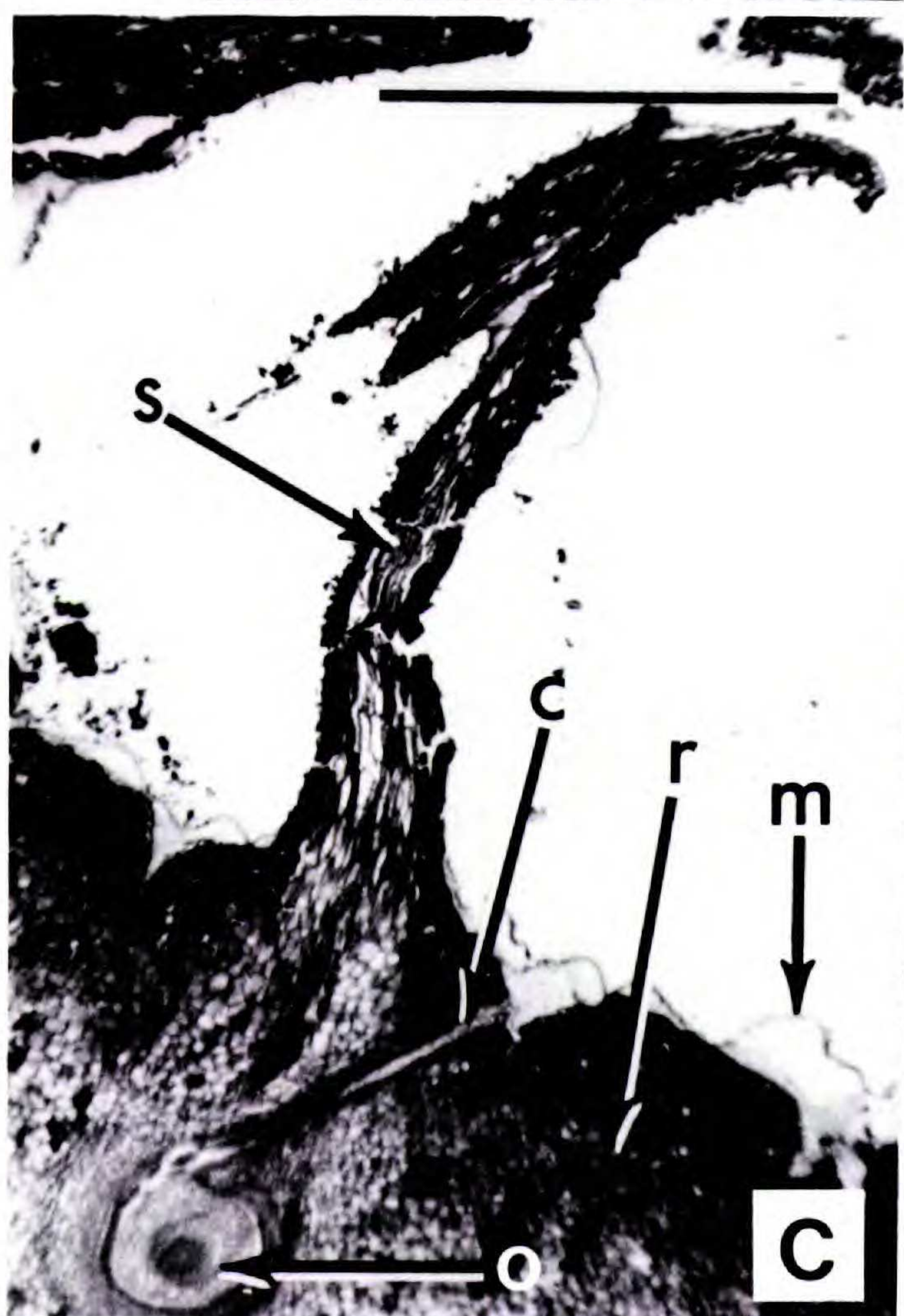
(*T. alaticarpa* and *T. longicarpa*) also possess this type of carpel (Fig. 16A). The inner receptacle surface may be glabrous (e.g., *T. tau*; Fig. 16C) or interspersed with dense tufts of short, simple lignified trichomes (e.g., *T. sieberi*; Fig. 16D).

The number of carpels varies greatly between species, is proportional to the size of the receptacle, and provides a good, species-specific character (Table 6). For example, fresh flowers of *T. purpurea* are only 5–6 mm diam. and have 35–70 carpels, whereas those of *T. ficus* are 35–40 mm diam. and have ca. 1,000–2,000 carpels. Size and shape of the styles are constant and often species-specific features, varying greatly within the genus. Styles of *T. peltata* (Fig. 16B) are short (ca. 0.5 mm long), crowded, and obtusely columnar. Those of *T. tau* (Fig. 16C) are longer (ca. 2–3 mm), free and setose, whereas in *T. sieberi* (Fig. 16D) they are 3–4 mm long, setose and coalescent. A canal was found to run obliquely upward from the ovule before opening at the base of the style in all 31 species examined in this study. This canal has been termed the “ventral slit” by Endress (1980b) and allows passage of the pollen tube for fertilization.

Pollen tube transmission in *Tambourissa* does not occur through the stylar tissue; rather, the site of transmission has shifted to the exterior of the style as in many other genera in the Monimiaceae (Endress, 1979, 1980b). In many species the entire external stylar surface is secretory, producing a mucilaginous exudate through which the pollen tubes grow until encountering the stylar canal and passing through it directly to the ovule. Traces of this mucilage can be seen in Figures 13E and 16C.

A further specialization is a massive mucilage production forming a thick layer lining the floral cup (e.g., *T. peltata*; Figs. 15A, 17E). This “extragynoecial compitum” functionally links and interconnects all the carpels (Endress, 1980b, 1982), enabling pollen grains deposited in one place to cross over and grow to any other carpel, thereby maximizing efficiency of the pollen. It is analogous to the usual intragynoecial compitum (transmitting tissue) in syncarpous gynoecia (Carr & Carr, 1961). The mucilage may also have a nectar function (see chapter on Floral Biology).

In *Tambourissa purpurea*, the extra-carpellary, stigmatic secretory epidermis covers not only the surface of the carpels but also the entire inner orifice of the floral cup including the inner tepals. Termed a “hyperstigma” by Endress (1979,



1980b; as *T. religiosa*), this unique floral construction is the culmination of floral specialization in Monimiaceae. In addition to *T. purpurea* it also occurs in *T. elliptica* and *T. crassa* (Lorence, pers. observ.), as well as *Wilkiea*, *Kibara*, and *Hennecartia*. (Endress, 1980b). In *T. purpurea*, a mucilaginous plug completely occludes the floral pore and forms a continuous layer extending down to the carpels and functions as the pollen reception and transmission site. In *T. crassa* and *T. elliptica*, the orifice is only occluded early in anthesis, but the mucilage otherwise completely lines the floral cup. A conspicuous mucilaginous exudate was also observed in fresh or rehydrated flowers of *T. decaryana*, *T. comorensis*, *T. longicarpa*, *T. madagascariensis*, *T. nosybensis*, *T. peltata*, and *T. beanjadensis* (Table 7).

Each *Tambourissa* carpel is supplied by a single vascular bundle dorsal to the ovule which runs into the style for much of its length. The carpels and receptacular ground tissue of each species characteristically contain varying proportions of one or more types of the following idioblasts: oil cells; tanniferous cells; stone cells. Amount and type of each provide useful, species-specific characters (Table 7).

Androecious flowers of all species of *Tambourissa* are globose to subglobose and closed in bud, usually bearing apically two external pairs of small to minute, free to fused tepals, and one or more additional pairs enclosed in the receptacle. The presence of tepals (as "staminodes") on inner receptacle lobes of the species formerly included in *Phanerogonocarpus* occurs in many species of *Tambourissa* and does not serve to distinguish the two genera as stated by Cavaco (1957c). The external receptacle surface is comparable to that of the gynoecious flower, ranging from glabrous to densely pubescent or corky. Male floral size shows great intraspecific variation, but is often comparable to that of the gynoecious receptacle. Two of the Comorean species, *T. kirikii* and *T. moheliensis* (Figs. 18D, 36D, E) have androecious receptacles that are much smaller than the gynoecious ones, however. The number of stamens is likewise proportional to receptacle size, and is generally somewhat less than the number of carpels in a given species (Table 6).

To cite extremes, fresh androecious buds of *T. purpurea* are 5–6 mm diam. with 20–32 stamens, whereas those of *T. ficus* are 45–50 mm diam. and contain ca. 900–1,800 stamens, making it the largest androecious flower in the family!

At anthesis, androecious flowers of most *Tambourissa* species split open by longitudinal fissures between the tepals into generally four or sometimes five (range three to seven) subequal, valvate lobes. The number of lobes and degree to which they split and reflex provide useful, species-specific characters. For example, lobes of *T. pedicellata* (Figs. 17C, 18F) are shallowly fissured, incurved, and scarcely open more than halfway. Those of *T. amplifolia* (Fig. 18B) split about halfway and open flat, whereas those of *T. quadrifida* (Figs. 18I, 19B) split deeply to the base and recurve completely. In some, including *T. purpurea* (Fig. 18E) and Comorean species such as *T. moheliensis* (Fig. 18D), the floral cup merely splits by shallow fissures and remains relatively closed and globose. An extreme form occurs in *T. gracilis* and *T. paradoxa*, which do not split at all; a small pore flanked by tepals provides the only access to the stamens. Such minute, closed flowers and very large, open flowers probably represent highly specialized, extreme forms derived from a more generalized type, perhaps similar to that of *T. pedicellata*.

Stamens of many *Tambourissa* species (e.g., *T. pedicellata*; Fig. 18F) consist of a distinct, broad filament and two lateral, bisporangiate, longitudinally dehiscent, extrorse loculi beyond which the connective is often slightly prolonged. This relatively unspecialized type resembles those found in *Decarydendron* and some species of *Ehippiandra*. Other species of *Tambourissa* display a number of extreme and highly specialized trends. One trend is towards extreme staminal elongation and prolongation of the connective, e.g., in *T. capuronii* (Fig. 18C) with stamens 6–8 mm long. In *T. tau* (Fig. 18H), the loculi occur on extended lateral arms of the connective in the form of a "T." The loculi of *T. ficus* (Fig. 18G) have shifted to an abaxial position with the filament and prolonged connective thickened. In other species such as *T. amplifolia* (Fig. 18B) and *T. peltata* (Figs. 17D, 18A), the loculi are often apically confluent and dehiscence

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FIGURE 16. Styles and carpels of some *Tambourissa* species, longitudinal sections.—A. *T. longicarpa*, Capuron 8775-SF (P).—B. *T. peltata*, Lorence 2555 (MO).—C. *T. tau*, Lorence 2953 (MO).—D. *T. sieberi*, Lorence 2250 (MO). Bars equal 1 mm. c = canal leading to ovule; m = mucilaginous exudate; o = ovule; r = receptacular ground tissue; s = style; t = trichome.

TABLE 6. Selected floral morphological features of *Tambourissa* species according to Group.

Species	Group	Sex	Androecious Flower		Stamens		Gynoecious Flower		Styles	
			Shape at Anth.		Conne- tive	Loculi	Shape	Orifice	No. (ca.)	Shape
<i>T. thouvenotii</i>	1A	monoec.	4-fid, flat		prol.	free	napiform- depressed	4-lobed	100– 150	conical
<i>T. trichophylla</i>	1A	monoec.	4-fid, flat		prol.	free	subglobose	4-lobed	100	conical
<i>T. uapacifolia</i>	1A	dioec.?	4-fid, flat		apic.	free	?	?	?	conical
<i>T. decaryana</i>	1B	dioec.?	?	?	?	?	napiform- depressed	4–5-lobed	200– 300	conical
<i>T. hildebrandtii</i>	1B	monoec.	4-fid, flat		prol.	free	napiform- subglobose	4-lobed	150– 200	conical
<i>T. humbertii</i>	1B	dioec.?	?	?	?	?	napiform- depressed	4(–5)-lobed	500	ovoid
<i>T. nitida</i>	1B	monoec.	?	?	apic.	free	napiform- turbinate	?	200†	conical
<i>T. nosybensis</i>	1B	monoec.?	4-fid, flat		apic.	free	discoid- patelliform	4-lobed	400	conical
<i>T. floricosata</i>	1C	monoec.	4-fid, in- curved		apic.	free	globose- depressed	subcirc.	?	conical
<i>T. parvifolia</i>	1C	monoec.	4-fid, flat		apic.	free	subglobose- napiform	subcirc.	200†	conical
<i>T. beanja- densis</i>	2A	monoec.	4–5-fid, flat		non-prol.	confl.	globose- napiform	4-lobed	200	conical
<i>T. comorensis</i>	2A	monoec.	4-fid, flat		non-prol.	free	patellif.- urceol.	circul., en- tire	200†	columnar
<i>T. crassa</i>	2A	dioec.	4–5-fid, ± flat		non-prol.	confl. (free)	subglobose- depressed	4(–8)-lobed	200†	columnar
<i>T. elliptica</i>	2A	monoec.	4-fid, flat		non-prol.	free (confl.)	globose- depressed	4-lobed	150– 200†	columnar

TABLE 6. Continued.

Species	Group	Sex	Androecious Flower		Stamens		Gynoecious Flower		Styles	
			Shape at Anth.	No. (ca.)	Connec- tive	Loculi	Shape	Orifice	No. (ca.)	Shape
<i>T. leptophylla</i>	2A	monoec.	4-fid, flat	80–90	apic.	free	globose-depressed	circul., en-tire	300–600	conical
<i>T. madagas-</i> <i>cariensis</i>	2A	dioec.?	4-fid, flat	200	apic.	free	subglobose-depressed	circul., en-tire	200†	columnar
<i>T. kirkii</i>	2B	monoec.	3-fid, subglobose	50?	prol.	free	patellif.-urceol.	circul., en-tire	200	conical
<i>T. paradoxa</i>	2B	dioec.?	globose, with small pore	40–50	prol.	free	?	?	?	?
<i>T. capuronii</i>	3	monoec.	4(–5)-fid, flat	300	prol.	free	napiform-depressed	±6-lobed	200†	conical
<i>T. moheliensis</i>	3	monoec.	4-fid, closed, subglobose	50	prol.	united basally	napiform-depressed	4-lobed	100–200	conical
<i>T. gracilis</i>	4	dioec.?	globose, with small pore	50	non-prol.	confl.	?	?	?	conical
<i>T. purpurea</i>	4	monoec.	globose, with small 3–4-lobed pore	20–32	non-prol.	confl.	globose	small, 3–4-lobed	35–70	columnar
<i>T. religiosa</i>	4	monoec.	closed? 4-lobed	50–75	apic. (non-prol.)	free-conniv.	napiform-depressed	4-lobed	300	conical
<i>T. amplifolia</i>	5	monoec.	4-fid, flat	100–250	non-prol.	confl.	napiform-discoïd	4-lobed	300	conical
<i>T. cocottensis</i>	5	monoec.	4–7-fid, flat	150–200	prol.	free	napiform-depressed	5–7-lobed	150–200	setose
<i>T. cordifolia</i>	5	dioec.	4-fid, flat	300–400	non-prol.	free-confl.	napiform-urceolate	4-lobed	100–400	conical

TABLE 6. Continued.

Species	Group	Sex	Androecious Flower		Stamens		Gynoecious Flower		Styles	
			Shape at Anth.	No. (ca.)	Con- nec- tive	Loculi	Shape	Orifice	No. (ca.)	Shape
<i>T. pedicellata</i>	5	monoec.	4(–6)-fid, half closed	50–70	non-prol.	free	subglobose	4–7-lobed	60–180	conical
<i>T. tau</i>	5	monoec.	4–5-fid, flat	100–150	apic. (non-prol.)	free	subglobose-urceolate	5–10-lobed	80–100	setose
<i>T. tetragona</i>	5	dioec.?	?	?	?	?	napiform-depressed	4-lobed	200	conical
<i>T. bathiei</i>	6	monoec.	3–4-fid, flat	350–450	non-prol.	free-confl.	globose	?	200†	conical
<i>T. sieberi</i>	6	monoec.	(4–)5-fid, flat	100–140	apic. (non-prol.)	free	globose	subcirc., small	850–875	setose
<i>T. perrieri</i>	7	monoec.	4-fid, flat-recurved	150–200	non-prol.	free	obovoid-obpyrif.	4-lobed, small	200	conical
<i>T. quadrifida</i>	7	monoec.	4-fid, flat-recurved	300–500	non-prol.	free	oblong-ellipsoid	3–4-lobed, very small	200–300	conical
<i>T. alaticarpa</i>	8	monoec.	4-fid, flat	38	non-prol.	free	cylindrical	6–8-lobed	250–300	conical
<i>T. longicarpa</i>	8	monoec.	4-fid, flat	40–50	prol.	free	cylindrical	4–6-lobed	300	conical
<i>T. castri-delphinii</i>	9	dioec.?	4–5-fid, flat-recurved	200–300	non-prol.	confl.	napiform-depressed	X-shaped	500–800	conical
<i>T. ficus</i>	9	monoec.	5–7-lobed, urceolate or flat	900–1,800	prol.	free (± unilateral)	urceolate	6–8-lobed	900–1,000–2,000	setose
<i>T. peltata</i>	9	dioec.	4–5-fid, flat-recurved	200–400	apic. (non-prol.)	free-confl.	discoid	4–7 flat lobes	400–500	flat, columnar (crowded)

is continuous. In *T. purpurea* (Fig. 18E), locular confluence is accompanied by an extreme staminal shortening and broadening, the resulting stamens being sessile or subsessile (0.7–1.2 mm long) with a single, crescentiform loculus which dehisces apically (Endress, 1980b; as *T. religiosa*) as in some species of *Ehippiandra*. However, basal fusion of the loculi occurs only in *T. mohe-liensis* (Fig. 18D), and also in some (but not all) stamens of *T. cordifolia* (Fig. 42C–E).

Anatomically, the androecious receptacle is similar to that of the gynoecious one. A single vascular bundle supplies each stamen (e.g., in *T. tau*). The same types of idioblasts are often found in the androecious flowers as in the gynoecious ones, most commonly oil and tanniferous cells. Stone cells, however, tend to be less abundant or lacking in the androecious flowers, e.g., *T. purpurea* (Endress, 1980b; as *T. religiosa*). Their greater abundance in gynoecious flowers and fruits suggests they may play a role in protecting the developing ovules from predation.

Floral color is relatively constant in many species, but quite variable in others (Table 8) which often have two color morphs. Flower color is always constant on a given individual and frequently constant within a local population. In *T. quadrifida*, however, both color morphs were observed in a single population at Yemen Valley, Mauritius. Incidentally, floral odor was found to be quite constant for each species and provides a diagnostic field character. Floral morphology, color, and odor all appear to be related to pollination syndromes (see discussion under Floral Biology).

In summary, floral size and morphology, including number, structure, and color of stamens in the androecious flowers and number, structure, and color of the styles in the gynoecious flowers are distinctive for most species of *Tambourissa*. These features provide some of the most taxonomically useful characters in the genus and should be recorded in the field notes. As flowers lose their shape upon drying, supplementary collections of flowers in alcohol should also be made whenever possible, as well as a photographic record. For a more detailed study of the floral morphology and anatomy of *Tambourissa*, see Endress and Lorence (1983).

FRUITING RECEPTACLE AND CARPELS

The seed-like fruiting carpels of all the genera for which information is available are fundamentally similar in being drupaceous and inde-

hiscent with a lignified endocarp, an abundant, oily endosperm, and a small embryo. While much larger in fruit, the shape of the receptacle and the carpels' position largely correspond with their shape and position in flower; i.e., significant generic differences exist. Also, the thick, pitted, bony white endocarp of *Monimia* (Monimioideae sensu Thorne, 1974) differs conspicuously from the thinner, finely sculptured, brownish, horny endocarps of the genera in Mollinedioideae (e.g., *Ehippiandra* and *Tambourissa*; unknown in *Decarydendron*).

Fruiting receptacles of all three species of *Monimia* are similarly subglobose to ovoid, enclosing from one to 12 free, seed-like drupaceous carpels. On herbarium labels these are often mistaken for multiple-seeded fruits. Fruiting receptacles of *Monimia* are strikingly similar to those of *Palmeria* (Corner, 1976; Endress, 1980b). At maturity the receptacle splits longitudinally from the apex into three to six irregular, valvate lobes that open to reveal the bright orange fruiting carpels set against the pinkish red receptacular surface (Figs. 14C, D, 19C). Birds appear to be the effective seed vectors for *M. ovalifolia* in Mauritius (Lorence, pers. observ.), and also for the species of *Monimia* in Réunion (A. Rolland, pers. comm.).

The indehiscent carpels of *Monimia* consist of a lignified, bony endocarp enveloped by a soft, orange, aril-like outer coating apparently composed of two distinct elements. The outermost is an enation extending downward from the stylar base over the apical portion of the carpel and forming a cap-like structure covering the lateral portions of the carpel, while leaving the dorsal and especially the ventral portion exposed (Fig. 19A, B, D). This outgrowth contains numerous oil cells and appears to represent an arilloid structure. The inner layer consists of the mesocarp proper which completely surrounds the endocarp, but is thickest basally (Fig. 19A, B, D). It is also orange but lacks the oil cells of the former. An analogous situation occurs in the neotropical *Siparuna* (Corner, 1976; Endress, 1973), and has been termed a "carpellary aril" or "stylar aril" respectively by these authors. Further studies on the development of *Monimia* carpels are in progress (Endress & Lorence, in prep.).

The endocarp of *Monimia* is whitish, irregularly ovoid-compressed, longitudinally crested and apically mucronate with the micropyle passing through the base of the beak. The wall is hard and bony, ca. 0.5–2 mm thick (probably adequate to survive passage through a bird's gut),

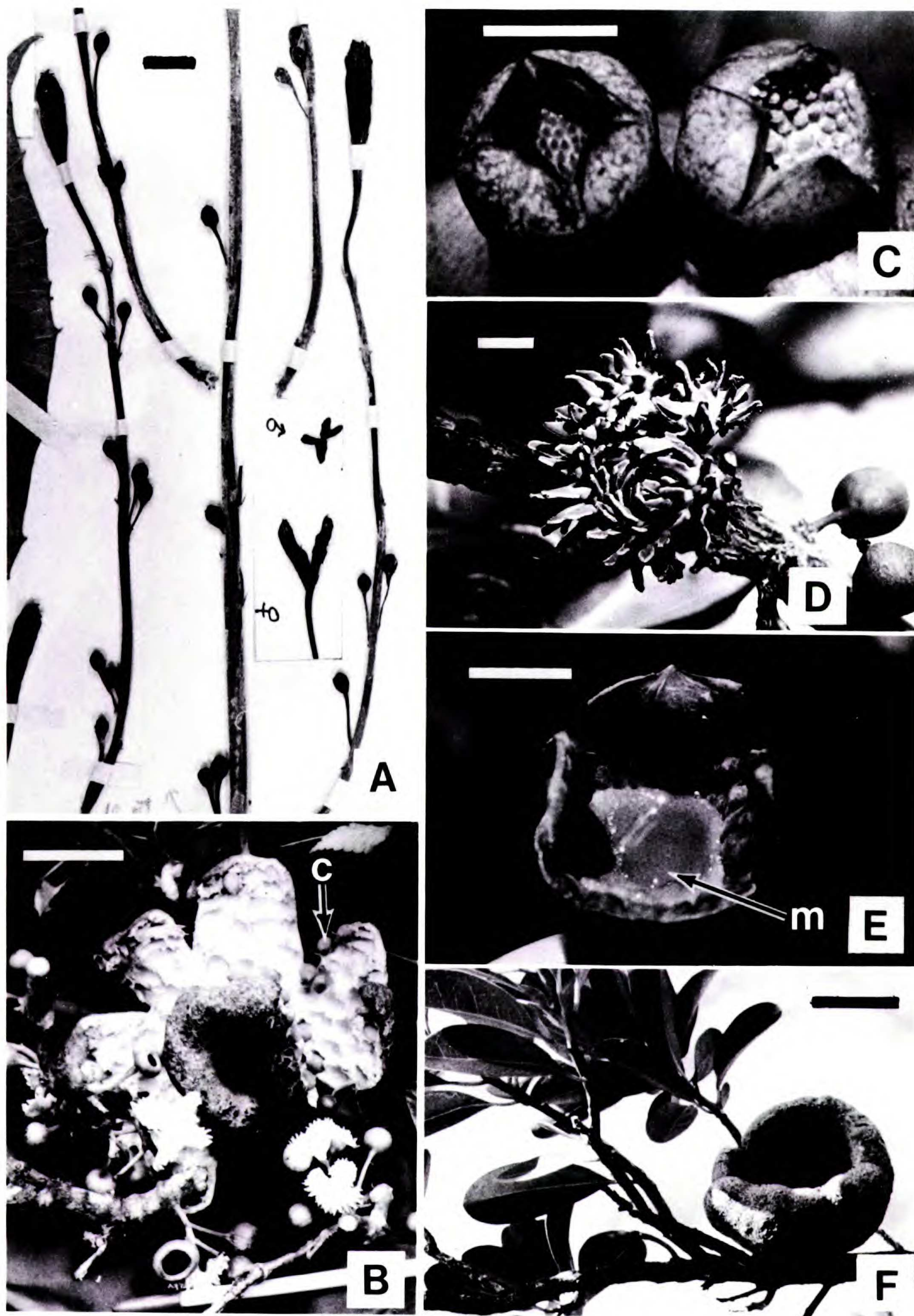


FIGURE 17. Flowers and fruits of some *Tambourissa* species.—A. *T. alaticarpa*, inflorescences showing terminal gynoecious flowers and lateral androecious flowers in bud, inset shows androecious flower at anthesis and longitudinally sectioned gynoecious flower, *Perrier de la Bâthie* 10102 (P).—B. *T. comorensis*, inflorescences with androecious and gynoecious flowers, and dehiscid fruiting receptacle exposing ripe carpels (c), *Lorence*

TABLE 7. Selected floral anatomical features of *Tambourissa* species according to Group. Data given for both androecious and gynoeceious flowers, except where noted. ± indicates presence of a small amount.

Species	Group	Tanniferous Idioblasts	Stone Cells (Sclerids)	Oil Cells	Mucilaginous Compitum (Gynoeceious)
<i>T. thouvenotii</i>	1A	+	—	—	—
<i>T. trichophylla</i>	1A	—	+	+	—
<i>T. uapacifolia</i> (♂)	1A	—	—	+	?
<i>T. decaryana</i>	1B	—	+	+	+
<i>T. hildebrandtii</i>	1B	+	—	+	—
<i>T. humbertii</i>	1B	—	—	+	—
<i>T. nitida</i>	1B	+	—	+	?
<i>T. nosybensis</i>	1B	—	+	+	+
<i>T. floricostata</i>	1C	+	—	+	?
<i>T. parvifolia</i>	1C	—	+	+	?
<i>T. beanjadensis</i>	2A	—	+	+	±
<i>T. comorensis</i>	2A	—	+	+	±
<i>T. crassa</i>	2A	—	—	+	+
<i>T. elliptica</i>	2A	±	+	—	+
<i>T. leptophylla</i>	2A	—	+	+	—
<i>T. madagascariensis</i>	2A	+	+	+	±
<i>T. kirkii</i>	2B	?	?	?	— (?)
<i>T. paradoxa</i> (♂)	2B	—	+	+	?
<i>T. capuronii</i>	3	+	+	—	—
<i>T. moheliensis</i>	3	+	+	±	—
<i>T. gracilis</i> (♂)	4	—	—	+	?
<i>T. purpurea</i>	4	+	+	—	+
<i>T. religiosa</i>	4	+	+	—	— (?)
<i>T. amplifolia</i>	5	+	+	+	—
<i>T. cocottensis</i>	5	+	+	—	—
<i>T. cordifolia</i>	5	+	+	—	—
<i>T. pedicellata</i>	5	—	+	+	—
<i>T. tau</i>	5	+	+	+	—
<i>T. tetragona</i>	5	+	—	+	—
<i>T. bathiei</i>	6	+	+	+	—
<i>T. sieberi</i>	6	—	+	+	—
<i>T. perrieri</i>	7	—	+	+	—
<i>T. quadrifida</i>	7	+	+	—	—
<i>T. alaticarpa</i>	8	+	+	—	—
<i>T. longicarpa</i>	8	+	+	+	±
<i>T. castri-delphinii</i>	9	+	+	+	—
<i>T. ficus</i>	9	+	+	+	—
<i>T. peltata</i>	9	+	+	—	+

and consists of many layers of contiguous sclerids. The endocarp surface is externally deeply pitted as in *Peumus* and *Siparuna*. Surface sculpturing ranges from foveate to reticulate or sulcate, varying even within a single species. Inside, a thin single-layered tegmen composed of elongated, rectangular cells encloses the abundant, oily endosperm. The small embryo is situated near the micropyle (Fig. 19A) and has slightly divaricate cotyledons. Germination of both *M.*

←
2870 (MO).—C. *T. pedicellata*, gynoeceious (left) and androecious (right) flowers at anthesis, *Lorence 2384* (MO).—D. *T. peltata*, androecious flower at anthesis and two androecious buds, Perrier Nature Reserve, Mauritius (R. E. Vaughan, unvouchered photo).—E. *T. peltata*, newly opened gynoeceious flower, note copious mucilaginous exudate (m) on gynoeceial disc, *Lorence 2555* (MO).—F. *T. peltata*, submature fruiting receptacle on branch, *Lorence 2197* (MO). Bars equal 10 mm in A, C–E, and 50 mm in B, F.

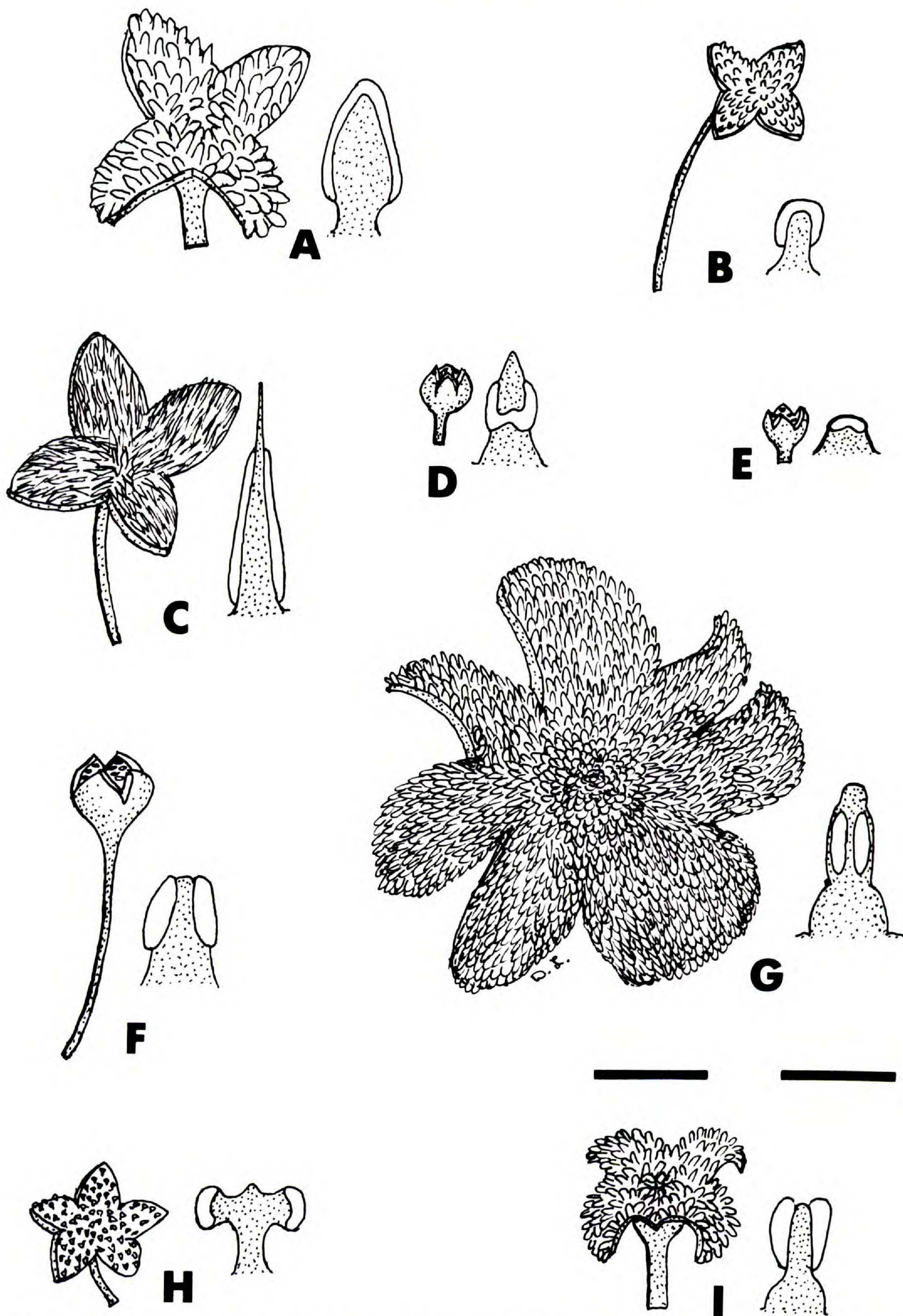


FIGURE 18. Androecious flowers and stamens of some *Tambourissa* species, drawn to approximate scale.—A. *T. peltata*.—B. *T. amplifolia*.—C. *T. capuronii*.—D. *T. moheliensis*.—E. *T. purpurea*.—F. *T. pedicellata*.—G. *T. ficus*.—H. *T. tau*.—I. *T. quadrifida*. Bar equals ca. 10 mm for flowers and ca. 1 mm for stamens.

TABLE 8. Floral color morphs of individuals of some species of *Tambourissa* from Mauritius and Réunion (inner receptacle surface, stamens or styles).

Species	Androecious Flower Color	Gynoecious Flower Color
<i>T. amplifolia</i>	white	orange; pale yellow
<i>T. cordifolia</i>	white	pink; purple-red
<i>T. crassa</i>	pale yellow; dark purple-red	pale yellow-green; dark purple-red
<i>T. elliptica</i> subsp. <i>elliptica</i>	white; pink	pale yellow-green; pink
<i>T. ficus</i>	white; purple-red	yellow-pink
<i>T. peltata</i>	purple-red; salmon pink	lobes purple-red, disc orange
<i>T. quadrifida</i>	orange; red	greenish white; reddish pink
<i>T. sieberi</i>	pale yellow; purple-red	pale yellow-green; purple-red
<i>T. tau</i>	greenish white; purple-red	purple-red

ovalifolia and *M. rotundifolia* seeds took over four months and viability was quite low, ca. 10–15%.

Fruiting carpels of *Decarydendron* are unknown (Cavaco, 1959). Because its flowering carpels are free and subsessile on the receptacular surface, the fruiting carpels may resemble those of *Ehippiandra* in being free and exposed on the receptacle, but probably lack a basal cupule and are sessile or shortly stalked as in *Hedycarya* or *Mollinedia*.

Mature fruiting receptacles of *Ehippiandra* (including *Hedycaryopsis*) are discoid, flat to convex, fleshy and red when fresh, and bear ca. 10–75 free, ovoid to ellipsoid carpels ca. 7–12 mm long. Each is partly surrounded basally for about one-third to one-half its length by a cupule (Fig. 14H) derived from the receptacle. The mature carpels are composed of a thin, fleshy green exocarp which turns black on ripening and surrounds the thin, pale brown, horny endocarp. The endocarp surface is smooth and finely scrobiculate as in *Tambourissa* and encloses a copious, fleshy endosperm.

As in the other genera, fruiting receptacles of *Tambourissa* (including *Phanerogonocarpus*) are many times larger than the flowers but otherwise similar in shape, ranging from flat and discoid (e.g., some *T. peltata* fruits), or somewhat open and cupuliform in the majority (e.g., Figs. 17B, F, 42J), to ellipsoid and closed with a small orifice in *T. quadrifida*, or cylindrical with four to five prominent external ridges in *T. alaticarpa* and *T. longicarpa*. The majority are corky brown externally, but may be smooth and dark (reddish when fresh) in *T. purpurea* and *T. religiosa*. Most have an internal cavity, but some fruits of *T. hildebrandtii* are almost solid. The styles persist in fruit and line the cavity, providing important

diagnostic features as to their size, shape, and number. Other taxonomically useful features of the fruiting receptacle are its position on the plant (on the trunk, branches, or terminal), whether solitary or in clusters, its size, shape, and the proportional size of the orifice.

At maturity the receptacle splits open irregularly, exposing the numerous, bright red-orange

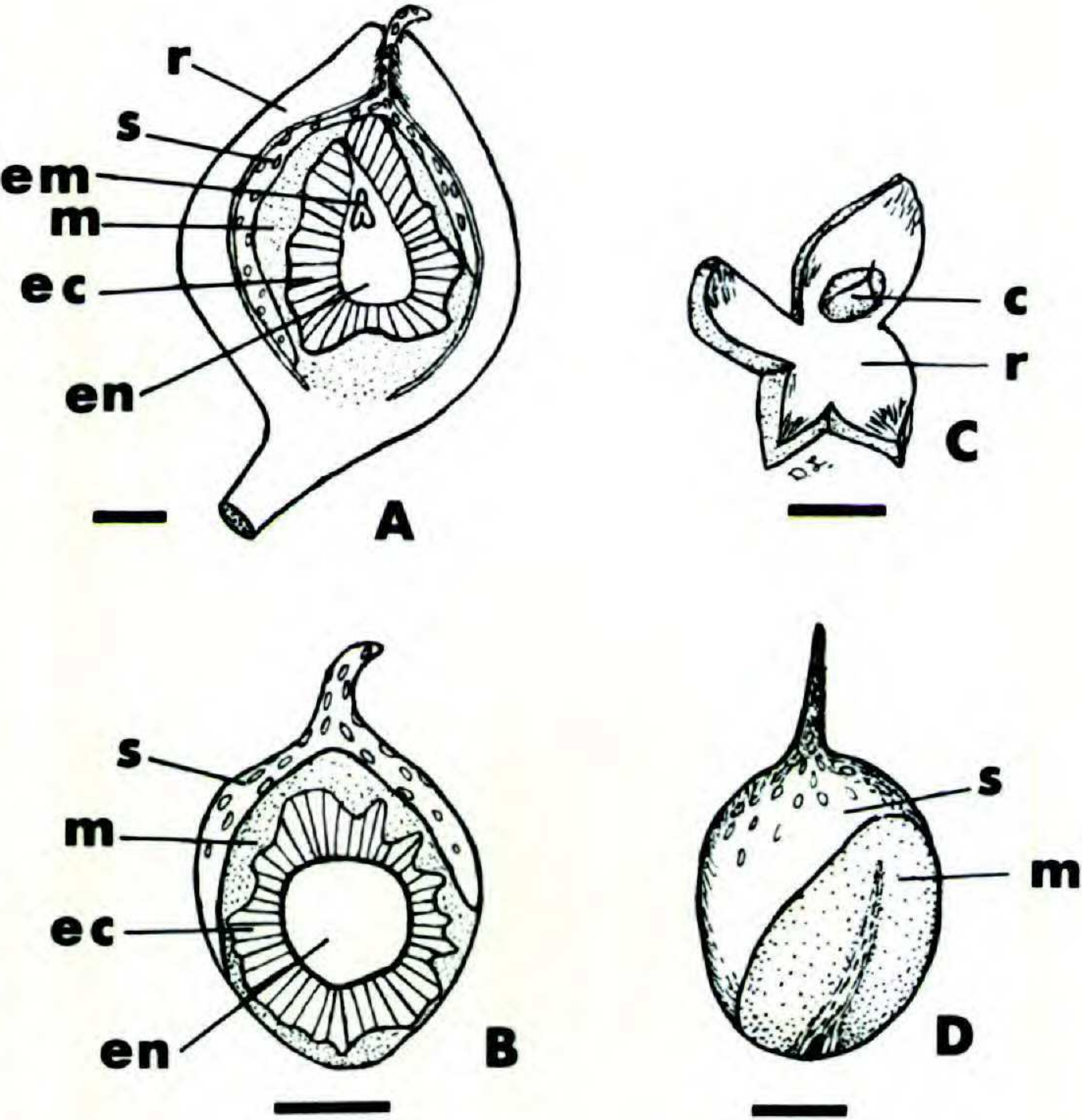


FIGURE 19. *Monimia* fruiting receptacles and carpels.—A. *M. ovalifolia*, submature fruiting receptacle with single carpel, longitudinal section, Lorence 2350 (MO).—B. *M. ovalifolia*, mature fruiting carpel, longitudinal section, Lorence 2350 (MO).—C. *M. amplexicaulis*, ripe receptacle split open to reveal single carpel, Lorence 2503 (MO).—D. *M. amplexicaulis*, ripe fruiting carpel, abaxial view, Lorence 2503 (MO). Bars equal 2 mm in A, B, D, and 10 mm in C. c = carpel; ec = endocarp; em = embryo; en = endosperm; m = mesocarp; r = receptacle; s = stylar aril.

carpels which separate from the pale orange receptacular ground tissue (Fig. 17C). In *Tambourissa cordifolia* (Lorence 2630, MO), the receptacle consists of parenchymatous ground tissue intermixed with sheets and columns of tanniferous cells and brachysclerids comprising nearly half the total tissue mass. In carpels of *T. cordifolia* the mesocarp is composed of parenchymatous cells containing numerous orange plastids interspersed with abundant oil cells and has a sweet taste when fresh (D. Lorence, pers. observ.). Beneath the mesocarp lies a horny, brown endocarp with a smooth, finely sculptured surface composed of numerous subspheroidal to cuboidal, lignified sclerids united into longitudinal bands and overlain by a single outer layer of flat, discoid sclerids. Beneath this lies an endotesta of elongated, annular tracheids three to four cell layers thick, and finally a unicellular tegmen of cuboidal cells surrounding the abundant endosperm whose cells are full of oil droplets. The embryo is 3–4 mm long, situated apically near the micropyle, and has two flat, erect cotyledons.

Carpels of various species differ somewhat in size and also color and sculpturing of the endocarp. In three Mauritian species belonging to Group 5 (i.e., *Tambourissa amplifolia*, *T. pedicellata*, and *T. tau*), it has sparsely branched, longitudinal ridges. Otherwise the carpels provide few taxonomically useful characters. Birds appear to be the effective seed vectors in *Tambourissa* (D. Lorence, pers. observ.; A. Rolland, pers. comm.; Benson 142, BM).

In summary, morphological and anatomical features of the wood, stems and phyllotaxy, leaves, inflorescence, flowers, and fruits of the Malagasy Monimiaceae often display marked trends and provide important diagnostic characters at the generic level. Furthermore, features of trichomes, inflorescence, and in particular floral morphology and anatomy also provide valuable diagnostic features at the specific level.

POLLEN

As a detailed palynological study of the Malagasy Monimiaceae has been published elsewhere (Lorence et al., 1984), only a brief summary of the results will be given here.

The four genera studied here all possess inaperturate spheroid, subspheroid, or ovoid pollen characteristic of the majority of the Monimiaceae sensu stricto excluding the Atherospermoideae, whose pollen is disulcate (Money et al.,

1950; Walker, 1976). Although Walker (1976) probably meant to exclude the spinose pollen of *Monimia* (Monimioideae), his statement that pollen of "... most of the genera on Madagascar and the Mascarenes is distinctive in possessing spiral bands on the surface" in the manner of *Hortonia* (Hortonioideae; Ceylon) does not accurately describe the pollen of the other three genera (all Mollinedioideae). Their sexines exhibit variable patterns ranging from spinose in *Monimia*, corrugate in *Decarydendron*, either granulate, reticulate, striato-rugulate, striato-reticulate, or tectate in *Tambourissa* (including *Phanerogonocarpus*), to granulate with verrucate, gemmate, or even vesiculate processes in *Ehippiandra* (including *Hedycaryopsis*) (Lorence et al., 1984).

It was found that pollen size, exine thickness, and sexinous patterns appear to provide useful, species-specific characters in the majority of species examined in this study. Although palynological evidence does not support the segregation of *Hedycaryopsis* from *Ehippiandra*, nor of *Phanerogonocarpus* from *Tambourissa*, generic differences in pollen are otherwise distinctive.

CHROMOSOME NUMBERS

As chromosome numbers provide some degree of support for the segregation of at least some of the subfamilies of Monimiaceae (e.g., Ehrendorfer et al., 1968; Goldblatt, 1974), and because all of the genera in the Malagasy region were previously unknown cytologically, it was decided to accumulate as much chromosomal information as possible during this study. All the reported counts were obtained from androecious flower buds fixed in 3 : 1 absolute ethanol : glacial acetic acid and later examined by the acetocarmine squash method.

Chromosomal study of all three species of *Monimia* has proven extremely difficult because of their small size and high number, a difficulty compounded by their tendency to stick together and by the presence of cytoplasmic inclusions. As a result, only approximate counts were obtained, both for *Monimia rotundifolia*: Réunion, Bébou cloud forest, Lorence 2429 (MO), $n = \text{ca. } 44$; Réunion, Col de Bellevue, cloud forest, Lorence 2473 (MO), $n = \text{ca. } 48$. The gametic chromosome number for this species therefore lies somewhere between 40 and 50, and it is obviously paleopolyploid.

These chromosomal findings for *Monimia* do not appear to suggest any close numerical affinity with *Peumus* ($2n = 78$; Morawetz, 1981). Both genera appear to be polyploids, however, as opposed to the majority of Monimiaceae sensu stricto (P. Goldblatt, pers. comm.).

All nine species of *Tambourissa* examined cytologically in this investigation had a gametic chromosome number of $n = 19$ (Table 9).

Although six of the species were from Mauritius, a few from Grande Comore, Réunion, and Madagascar were also examined with the same results. This suggests that the extensive adaptive radiation of *Tambourissa* in the Malagasy region has occurred at the same chromosomal level.

The paleohexaploid base number $x = 19$ (Goldblatt, 1980) is shared with a number of genera from Oceania also belonging to Mollinedioideae sensu Thorne (1974)—i.e., *Hedycarya*, *Levieria*, *Palmeria*, and *Wilkiea* (Ehrendorfer et al., 1968)—as well as by *Hortonia* in the Hortonioideae (Goldblatt, 1974). As in *Tambourissa*, these genera are characterized by androecious flowers bearing numerous, irregularly spaced subsessile stamens with lateral dehiscence (Ehrendorfer et al., 1968), although gynoecious floral construction is more variable (Endress, 1980b). Similarities in cytology and androecious floral morphology among these genera suggest they are relatively closely allied within the Mollinedioideae.

The remaining endemic Madagascan genera belonging to the Mollinedioideae—i.e., *Decarydendron* and *Ephippiandra* (including *Hedycaryopsis*) as well as both *Tambourissa* species formerly included in *Phanerogonocarpus*—are unknown cytologically.

FLORAL BIOLOGY

Although the vegetative and floral anatomy (Money et al., 1950), palynology (Walker, 1976), and cytology (Ehrendorfer et al., 1968; Goldblatt, 1974) of various extant primitive angiosperm families have been relatively well studied, comparatively little is known of their floral biology and breeding systems. I have therefore attempted to accumulate as much data as possible on these aspects of the Monimiaceae while in the Malagasy area.

The only confirmed report on pollination in Monimiaceae sensu stricto is by Gottsberger (1977), who observed female thrips making holes and ovipositing in androecious and gynoecious

flower buds of *Mollinedia* in Brazil. The larvae develop and mature inside the buds and the adults emerge as the buds open, flying out and carrying pollen to other flowers as they seek mates. Endress (1979, 1980b) also reported finding holes and eggs in flowers of *Wilkiea* and *Stegnanthera* (Mollinedioideae), which may have been from pollinating insects. More recently, investigations by Thien (1980) on the pollination of species of primitive angiosperms belonging to the Degeneriaceae (*Degeneria*) and Winteraceae (*Drimys*, *Bellium*, and *Zygogynum*) in the South Pacific islands show that members of the orders Coleoptera, Diptera, Lepidoptera, and Thysanoptera are important pollinators of these plants.

The present study was conducted in Mauritius during 1978–1979 and includes observations on seven species of *Tambourissa* and one species of *Monimia*. The species studied, study sites, and observation periods are given in Tables 10 and 11. Insect visitors were captured, killed, and mounted or stored in 70% alcohol for identification. Flowers of all species studied were observed and photographed during various stages. Voucher specimens of the plants are deposited at MAU and MO.

Tambourissa is a genus of monoecious or dioecious shrubs, treelets, or trees. All species have highly specialized, unisexual flowers with minute, scale-like tepals, a well-developed receptacle which assumes the functions of a perianth and ovary wall, and inferior carpels. As an understanding of the floral morphology is essential to understand the pollination biology, this chapter should be read in conjunction with the section on floral morphology and anatomy.

Female receptacles of most species are somewhat globose and closed in bud, and split open at maturity into (3–)4–5(–10) lobes, depending on the species. Once open, they do not close again. The receptacle is lined with numerous short to long styles, each corresponding to a single carpel. These become receptive gradually and centripetally during floral anthesis, which typically lasts 10–15 days. Receptive styles of most species produce a slight mucilaginous exudate in which the pollen tubes germinate and grow (e.g., *Tambourissa tau*, *T. cordifolia*, Figs. 13E, 16C). In others, the styles are reduced and covered by a massive mucilaginous secretion (compitum) (e.g., *T. peltata*, Fig. 17E). In yet others (e.g., *T. purpurea*), the flower remains closed except for a mucilaginous plug which occludes the floral entrance and has a stigmatic function (Endress,

TABLE 9. Collections of *Tambourissa* in which the haploid chromosome number was determined as $n = 19$. All collections are mine; vouchers are deposited at MO and most at MAU also.

Species	Lorence Number	Locality
<i>T. comorensis</i>	2878	Grande Comore. La Grille, wet forest.
<i>T. cordifolia</i>	2571	Mauritius. Pétrin Nature Reserve, <i>Philippia</i> heath formation.
<i>T. elliptica</i>		
subsp. <i>elliptica</i>	2526, 2530	Réunion. Takamaka, wet forest.
subsp. <i>micrantha</i>	2483	Réunion. Mare Longue, wet forest.
<i>T. pedicellata</i>	2384	Mauritius. Pieter Both Mt., degraded wet forest.
<i>T. peltata</i>	2553	Mauritius. Cascade Alexandra, stunted wet forest.
<i>T. purpurea</i>	1726	Madagascar. Wild, locality unknown (cult. MO).
<i>T. quadrifida</i>	2539	Mauritius. Matala Valley (Yemen), semideciduous dry forest.
<i>T. sieberi</i>	2250	Mauritius. Mt. Cocotte Nature Reserve, cloud forest.
<i>T. tau</i>	1964	Mauritius. Piton de la Rivière Noire, wet forest.
<i>T. tau</i>	2951	Mauritius. Perrier Nature Reserve, wet forest.

1979, 1980b; as *T. religiosa*). This “hyperstigma” occurs in some Madagascan and Réunion species, but is absent from Mauritian and Comorean plants. The sweet mucilage of *T. purpurea* tested positive for reducing sugars with Benedict’s solution and for glucose with Lilly TES-tape (paper for analysis of urine sugar), respectively (Endress & Lorence, 1983). It therefore probably has a nectar function in a number of species that produce an abundant secretion (e.g., *T. crassa*, *T. elliptica*, *T. peltata*, *T. purpurea*). Flowers of most Mauritian species also produced strong floral odors which presumably attract pollinators.

Androecious flowers are similarly lined with numerous stamens that also mature gradually and centripetally after the globose receptacle splits into (3–)4–5(–7) subequal valvate segments. Although a few Comorean and Madagascan species open by a small apical orifice, lobes of most species open flat or even recurve and remain permanently open during their 7–12 day life span. Androecious flowers produce large amounts of pollen, which represent a substantial floral reward, although secretions are absent. In addition, floral odors like those in the gynoeceous flowers are emitted.

In the Mauritian *Tambourissa* species, from one to more than 100 flowers were found to be open on a given day, depending on the species and individual, and flowering generally occurred over a three to five month period. These aspects will be discussed below in more detail by species. A synopsis of the results of this study for *Tambourissa* in Mauritius is as follows.

1. Major pollinators are insects belonging to the orders Coleoptera and Diptera.
2. Gynoeceous floral morphology, notably size of the floral entrance, plays a key role in regulating insect entry.
3. Floral odor, and possibly also color, plays an important role in attracting pollinators.
4. Floral reward in the androecious flower is pollen. Gynoeceous flowers of some species attract by deceit, while in others a mucilaginous exudate seems to have a nectar function.
5. Demography, phenology, and breeding systems are related to pollinator syndromes.

TAMBOURISSA SIEBERI

Tambourissa sieberi, a large, monoecious canopy tree 8–10 m tall, is known from only a few restricted areas of mature wet and cloud forest in Mauritius. It is scarce and occurs as scattered individuals in low population densities, e.g., at Macabé forest (Table 4), and at Mt. Cocotte where it was studied (Table 10). Hundreds of flowers (16–90 per inflorescence) are produced in unisexual pleiochasia and thyrses arising in large numbers from the trunk and major branches from December to February.

Gynoeceous flowers are globose with a small apical pore only 2–3 mm diam. (Fig. 20A). Several hundred long styles which are coalescent into groups fill the receptacle, leaving only a small central cavity (Fig. 15E). The styles are moist at anthesis due to a slight surface exudate. Androecious flowers are relatively large and split into five spreading, reflexed lobes bearing ca. 100–

TABLE 10. Localities for pollination biology studies in Mauritius.

No.	Locality	Vegetation Type	Ele- vation (m)	Annual Pptn. (mm)	Date	Season
1.	Mt. Cocotte	cloud forest	760	5,000	Jan. 1979	wet
2.	Matala valley (Yemen)	semideciduous dry forest	200	1,600	June–July 1979	dry
3.	Perrier	<i>Sideroxylon</i> lower montane wet forest	600	3,400	Sept.–Oct. 1978 Sept. 1979 Apr. 1979	dry dry end wet
4.	Pétrin	<i>Philippia</i> heath formation	630	4,000	May 1979	start dry
5.	Bel Ombre	Lowland wet (high) forest	300	2,400	Dec. 1978–Jan. 1979	wet
6.	Mare Longue Plateau	Lower montane wet forest	660	3,400	Apr. 1979	end wet
7.	Piton Brise Fer	Lower montane wet forest	700	2,400	Dec. 1978	wet

140 large stamens that release abundant, coalescent pollen. Flowers may be either pale yellow or dark reddish purple, depending on the individual. Flowers of both sexes produce the same strong, cloying odor of overripe or fermenting fruit.

Observations made near midday, totalling 3.4 hours, revealed that introduced honeybees (*Apis mellifera*) were the most frequent visitors of androecious flowers, from which they gathered pollen. They showed no interest in the gynoecious flowers, however, nor could they enter them. Other less frequent visitors to the androecious flowers were unidentified Syrphidae (two species) and another unidentified dipteran (Table 11). No visitors were observed on the gynoecious flowers during this time, and no observations were made at night.

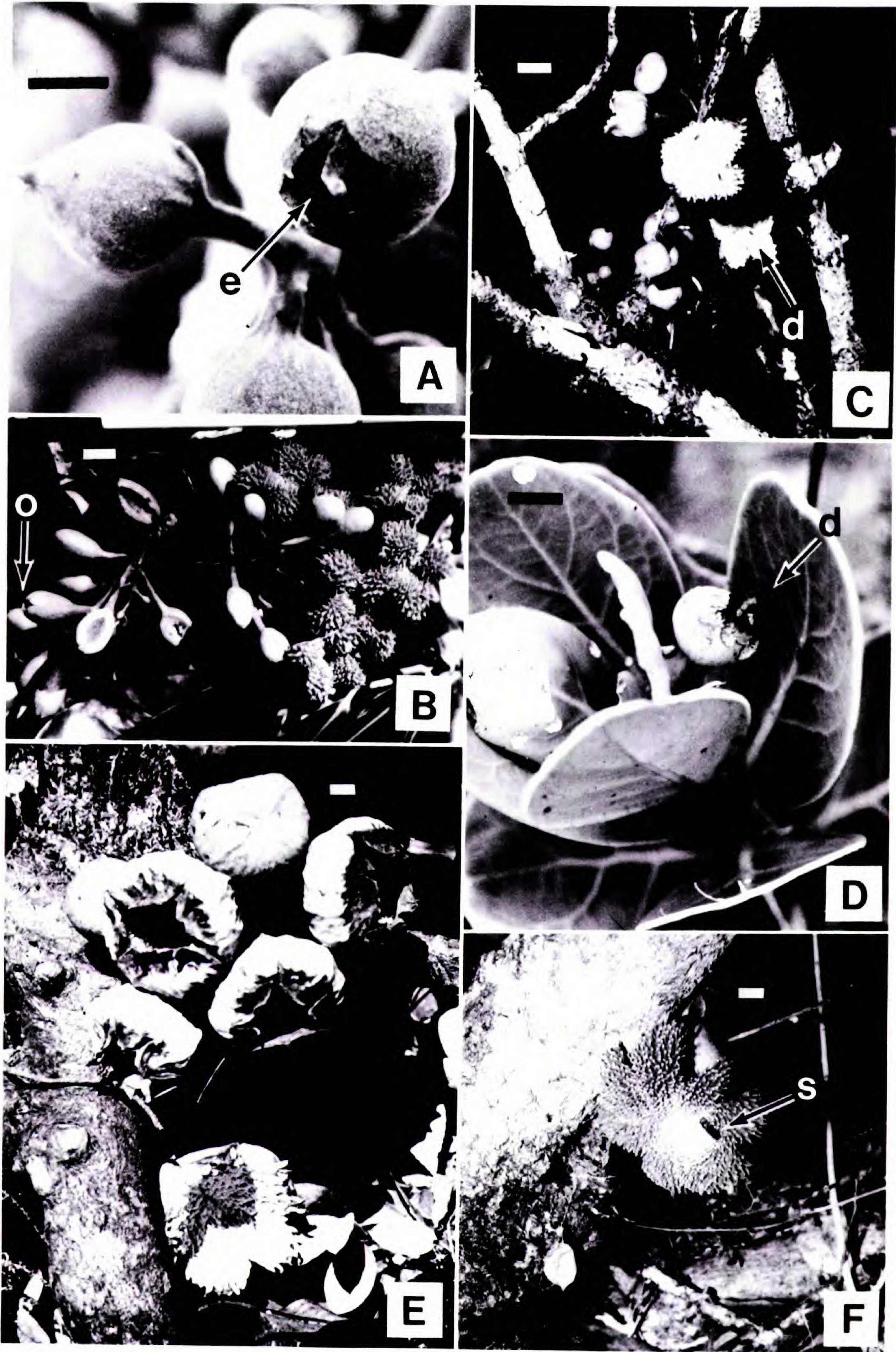
Examination of the contents of ten gynoecious flowers from the tree and 15 fallen flowers revealed the presence of various small arthropods, notably a variety of small Coleoptera only 2–3 mm long, in over half the flowers (Table 12). These Coleoptera, belonging to the families Hydrophilidae, Nitidulidae, Rhizophagidae, and Staphylinidae, are presumably active at night. They probably visit androecious flowers to feed on the pollen, attracted by the strong floral odors. They also enter the gynoecious flowers to feed on the styles, which were damaged in certain flowers, and probably oviposit there, as eggs and larvae were found in some flowers (Table 12). Because the stylar canal is situated near the style's base, damage to its terminal portion probably has little if any effect on pollen tube germination and growth which may occur anywhere on the stylar surface. Reduction of the floral entrance can be viewed as a strategy to protect the ovules

from damage by larger, more destructive beetles (cf. Gottsberger, 1974, 1977; Endress, 1980b), at the same time allowing access to the less destructive small beetles. Elongation and coalescence of the styles may provide food for the coleopterans and also protect the ovules. Carpel group formation of this type, by connivence of the styles and cohesion by the mucilaginous secretion, functionally divides the gynoecium into several subunits, each being composed of a number of carpels (Endress & Lorence, 1983). This phenomenon is unknown elsewhere among the angiosperms.

Breeding experiments suggest that *Tambourissa sieberi* is the only self-compatible monoecious species of the four tested in Mauritius (Table 13). I suspect self-compatibility in *T. sieberi* may be a strategy to offset its low population densities and probable inefficiency of the small pollinators. Production of a large number of flowers and a prolonged flowering period may also compensate for these factors.

TAMBOURISSA QUADRIFIDA

Tambourissa quadrifida is the only species of Monimiaceae to occur in the dry forest zone of Mauritius. A mid stratum or subcanopy tree, it occurs in small, scattered populations and readily forms multiple coppice stems. Individuals are subdioecious, producing flowers of predominantly one sex, and flower from June to August. The numerous flowers are produced in pleiochasia and thyrses along the trunk, and hundreds of flowers may be open on a given day, each persisting for ca. 10–15 days. During the 1979 flowering season, a predominantly androecious tree (Lorence 2656, MO) was estimated to produce nearly 24,000 flowers, and a predominantly gyn-



oecious tree (*Lorence 2655*, MO) over 15,000 flowers! Crossing experiments carried out on three individuals showed them all to be self-incompatible (Table 13).

The gynoecious flowers of *Tambourissa quadrifida* are ellipsoid to obovoid and open by a small apical pore only 1–2 mm diam. (Fig. 20B). Inside, 200–300 short, glistening pink or yellow styles line the hollow receptacle; only a small amount of stylar exudate is produced. The orange or red androecious flowers split into four ultimately recurved segments bearing 300–500 stamens with slightly coalescent pollen (Fig. 20B). A strong, pleasant odor of ripe fruit is produced by flowers of both sexes.

Studies were carried out on a population of four individuals at Yemen (Matala Valley) on the edge of a dry forest degraded by numerous exotics. Observations totalling 13.4 hours revealed that large numbers of small Diptera (*Drosophila* spp., *Homoneura*, and *Zaprionus*) congregated on the androecious flowers in the early morning, but did not enter the gynoecious flowers (Table 11). For this reason, the drosophilids presumably have little, if any, effect as pollinators. Three species of syrphids also visited the androecious flowers occasionally during the day to feed on the pollen, and pollen foraging activity by honeybees was also intense throughout the day. As these insects are all too large to enter the gynoecious flowers in which the styles are concealed, they cannot function as pollinators.

An examination of 438 gynoecious flowers from the tree and 132 fallen flowers revealed that 93.6% and 75.8% respectively were devoid of any contents (Table 14). A number contained mealybugs which were presumably brought in by the small ants also found in some flowers. Ants are probably ineffective as pollinators, as they did not visit androecious flowers. A small percentage of flowers contained silk webbing, often with small larvae or pupae (probably Lepidoptera). These larvae appeared to graze on the styles and probably represent predators, although pollinating activity by the ovipositing adults cannot

be discounted. The only likely pollinator observed was a small Nitidulidae beetle, *Haptoncus luteolus* (Tables 11, 14) seen emerging from a gynoecious flower. It subsequently visited an androecious flower to forage for pollen, which adhered to its body. The beetle is probably able to travel the short distances of several meters separating trees in this population. Significantly, another species of *Haptoncus* was seen in the structurally similar gynoecious flowers of *Tambourissa sieberi* (Table 12), and Thien (1980) found the same genus in *Degeneria* flowers.

One factor responsible for the scarcity of pollinators on *Tambourissa quadrifida* at Yemen may have been the disturbed, partly secondary nature of the habitat. However, the predominantly gynoecious tree of the four usually produces some fruit clusters each year (J. A. Lalouette, pers. comm.), indicating that effective cross pollination does occur to a certain degree.

As in *Tambourissa sieberi*, an extreme reduction of the gynoecious floral entrance excludes larger, more destructive insects, permitting only smaller pollinators like the nitidulid to enter. The tremendous floral production in *T. quadrifida* presumably offsets the lower efficiency of these insects as pollinators as in *T. sieberi*, whereas self-incompatibility and subdioecy would enforce outcrossing.

TAMBOURISSA TAU

Tambourissa tau is a slender, monoecious understory treelet rarely exceeding 2–3 m high. Flowers are produced from meristematic swellings along the main stem, or in the leaf axils. Depending on its size, each plant may produce over 100 solitary or fasciculate flowers over a three to five month period, but only several open at a time, each lasting for 10–15 days. Crossing experiments revealed it to be self-sterile (Table 13).

Gynoecious flowers are relatively small, externally corky, and split about half way open into 6–10 irregular, suberect lobes (Fig. 39E, F). Each

←

FIGURE 20. Flowers of some *Tambourissa* species.—A. *T. sieberi*, gynoecious flowers in bud (left) and at anthesis (right), note insect egg (e) in orifice, *Lorence 2250* (MO).—B. *T. quadrifida*, inflorescences with gynoecious flowers (left), note small orifice (o), and androecious flowers (right), *Lorence 2656* (MO).—C. *T. cordifolia*, androecious plant with flowers in bud and at anthesis, note visiting drosophilids (d), *Lorence 2632* (MO).—D. *T. crassa*, gynoecious flower at anthesis, note visiting dipteran (d) drinking mucilage, *Lorence 2468* (MO).—E. *T. ficus*, form with partly closed white androecious flowers in bud, at anthesis and post anthesis, *Lorence 1485* (MO).—F. *T. ficus*, form with open purple androecious flower at anthesis, note visiting syrphid (s), *Lorence 2115* (MO). Bars equal 10 mm.

TABLE 11. Pollination biological data for species of Monimiaceae in Mauritius.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
<i>Monimia ovalifolia</i>	1	10 Aug. 1979	11:30 A.M.– 1:40 P.M.	cloudy, rainy	16– 17.5	2.2	Diptera Syrphidae cf. <i>Isciodon</i> sp.	5	numerous
<i>Tambourissa amplifolia</i>	5	10 Jan. 1979	9:10 A.M.– 1:40 P.M.	sunny to rainy	26–30	4.5	Diptera Drosophilidae <i>Drosophila</i> cf. <i>nasuta</i> Lauxaniidae <i>Homoneura</i> sp.	1 3 0	6 ♀, 18 ♂ 6 ♀, 18 ♂ 9 ♂
<i>T. cordifolia</i>	4	12 May 1979	1:20 P.M.– 5:30 P.M.	sunny to rainy	26–22	4.2	none		
			6:30 A.M.– 11:30 A.M.	dawn to sunny & windy	18– 26.5	5.0	Diptera Drosophilidae <i>Drosophila nasuta</i> <i>Zaprionus vittiger</i>	total 72	9 ♂ 9 ♂
	4	13 May 1979	6:45 A.M.– 11:10 A.M.	dawn to sunny & windy	18– 26.5	4.4	Diptera Drosophilidae <i>Drosophila nasuta</i> Lauxaniidae <i>Pachycerina</i> sp.	total 12	6 ♀ 6 ♀
	4	19 May 1979	5:00 P.M.– 6:45 P.M.	sunny & windy to dusk	19.5– 16	1.8	Diptera Drosophilidae <i>Drosophila nasuta</i>	1	7 ♂
	4	30 May 1979	6:05 A.M.– 9:05 A.M.	dawn to sunny & windy	18–26	3.0	Diptera Drosophilidae <i>Zaprionus vittiger</i> Lauxaniidae <i>Homoneura</i> sp.	total 12	6 ♂ 6 ♂
	4	30 May 1979	6:45 A.M.– 11:15 A.M.	dawn to sunny & windy	19–26	4.5	Diptera Drosophilidae <i>Drosophila nasuta</i>	1	6 ♀

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
<i>Tambourissa ficus</i>	7	8 Dec. 1978	11:00 A.M.— 11:50 A.M.	fair	23.5– 25	0.8	Diptera Syrphidae <i>Eumerus</i> sp.	2	2 ♂
	1	12 Dec. 1978	8:45 A.M.	fair	—	spot check	Coleoptera Hydrophilidae <i>Cercyon</i> sp.	42	2 ♀, 1 ♂
<i>T. peltata</i>	6	10 Apr. 1979	7:30 A.M.— 11:30 A.M.	fair & occ. rain	20–27	4.0	Diptera Drosophilidae (unidentified) Syrphidae cf. <i>Askarina</i>	4	16 ♀
	6	19 Apr. 1979	3:45 P.M.— 5:30 P.M.	fair, sunny	25–21	1.8	Diptera (unidentified) Diptera Syrphidae (unidentified)	1 1	16 ♀ 16 ♀
	3	9 Apr. 1979	10:30 A.M.— 10:50 A.M.	fair	24–25	0.3	Diptera Syrphidae <i>Askarina</i> sp. Hymenoptera Apidae	1 3	12 ♀ 6 ♂
	3	9 May 1979	11:00 A.M.— 11:20 A.M.	fair	25	0.3	<i>Apis mellifera</i> Diptera (small, unidentified)	1 3	6 ♂ 2 ♀
	3	10 May 1979	3:45 P.M.— 4:00 P.M.	fair	28.5– 27	0.3	Diptera (small, unidentified)	1	2 ♀
	3	11 May 1979	3:20 P.M.— 4:00 P.M.	fair	28– 24.5	0.7	Hymenoptera Apidae <i>Apis mellifera</i>	3	8 ♂
	3	12 May 1979	8:15 A.M.— 9:00 A.M.	passing showers	22–23	0.8	Diptera Drosophilidae <i>Drosophila</i> (<i>melanogaster</i> grp.) <i>D. nasuta</i> <i>Zaprionus hibernaculatus</i> Syrphidae <i>Askarina</i> sp. <i>Ornida obesa</i>	many many many 1 2	25 ♂ 25 ♂ 25 ♂ 25 ♂ 25 ♂

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
<i>Tambourissa quadrifida</i>	2	20 June 1979	7:12 A.M.–	fair to	20–	4.5	Diptera		
			11:40 A.M.	cloudy	24.5		Drosophilidae <i>Drosophila</i> sp. <i>Zaprionus</i> sp. Syrphidae <i>Ornida obesa</i> Hymenoptera Apidae <i>Apis mellifera</i>	several 1 1 1 5	hundreds ♂ hundreds ♂ hundreds ♂ hundreds ♂
	2	21 June 1979	7:20 A.M.–	fair to	20–24	4.4	Diptera		
			11:45 A.M.	cloudy			Lauxaniidae (unidentified) Syrphidae (unidentified) Diptera	1 1	several ♂ several ♂
	2	22 June 1979	7:00 A.M.–	fair to	19.5–	4.5	Diptera		
			11:30 A.M.	cloudy	24		Drosophilidae <i>Drosophila nasuta</i> <i>D. (melanogaster</i> grp.) <i>Zaprionus</i> sp. Lauxaniidae <i>Homoneura quadrivittata</i> Syrphidae (2 spp., unident.) Coleoptera Nitidulidae <i>Haptoncus luteolus</i> Hymenoptera Apidae <i>Apis mellifera</i>	many many 2 3 3 1	hundreds ♂ hundreds ♂ hundreds ♂ hundreds ♂ hundreds ♂ 1 ♀
	1	4 Jan. 1979	11:00 A.M.–	fair to	28–29	1.2	Hymenoptera Apidae		
			12:12 P.M.	cloudy			<i>Apis mellifera</i>	6	hundreds ♂
	<i>T. sieberi</i>								

TABLE 11. Continued.

Species	Loc.	Date	Time	Weather	T° (C)	Total Obs. Time (hr.)	Insect Visitors/Pollinators	Max. Obs.	No. Flowers Observed
<i>T. tau</i>	1	4 Jan. 1979	12:45 P.M.— 1:55 P.M.	fair to cloudy	25.5— 24	1.2	Diptera Syrphidae (unidentif.) Diptera (unidentified)	3 1	many ♂ many ♂
	1	17 Jan. 1979	1:10 P.M.— 2:10 P.M.	cloudy	27— 23.5	1.0	Diptera Syrphidae (unidentified) Diptera (unidentified) Hymenoptera Apidae <i>Apis mellifera</i>	2 1 1	many ♂ many ♂ many ♂
	3	8 Oct. 1978	3:30 P.M.— 5:30 P.M.	fair to rainy	23.5— 22	2.0	Coleoptera Curculionidae <i>Scaevinus truncatus</i> <i>Scaevinus truncatus</i>	1 2	4 ♂ 1 ♂
	3	17 Oct. 1978	3:00 P.M.— 4:20 P.M.	fair	23—22	1.3	Coleoptera Curculionidae <i>Scaevinus truncatus</i>	2	1 ♂
	3	18 Oct. 1978	9:30 A.M.— 11:00 A.M.	fair	19.5— 22.5	1.5	Coleoptera Curculionidae <i>Scaevinus truncatus</i> <i>Scaevinus truncatus</i>	2 1	3 ♂ 1 ♂
	3	20 Oct. 1978	—	fair	—	spot check	<i>Scaevinus truncatus</i> <i>Scaevinus truncatus</i>	2 1	3 ♂ 1 ♂
	3	23 Oct. 1978	2:30 P.M.— 3:00 P.M.	fair	25—24	0.5	<i>Scaevinus truncatus</i>	2	2 ♂
	3	6 Dec. 1978	—	—	—	spot check	<i>Scaevinus truncatus</i>	1	1 ♂
	3	2 Sept. 1979	6:00 A.M.— 11:30 A.M.	fair to rainy	17—23	5.5	<i>Scaevinus truncatus</i>	1 (on ♀)	4 ♀, 4 ♂

TABLE 12. Contents of *Tambourissa sieberi* gynoecious flowers sampled at Mt. Cocotte, Mauritius in January 1979.

Contents	No. Flowers From Tree	% Total	No. Flowers From Ground	% Total
Empty	10	45.5	15	41.7
Small Coleoptera:	6	27.3	13	36.1
(Hydrophilidae, <i>Dactylosternum vinsoni</i> B.B.; Nitidulidae, <i>Carpophilus mutilatus</i> Er., <i>Epuraea terminata</i> Rtt., ^a <i>Haptoncus minutus</i> Rtt., <i>Lasiodactylus pictus</i> MacL.; Rhizophagidae, <i>Europs</i> cf. <i>brevis</i> Gronv.; Staphylinidae, <i>Atheta dilutipennis</i> Mots., <i>Philonthus flavocinctus</i> Mots.				
Lepidoptera (<i>Opogona sacchari</i> Bojer, larva, presumably a predator)	1	4.5	5	13.9
Unidentified larvae (possibly Diptera)	2	9.1	0	0
Ants (Hymenoptera, Formicidae)	0	0	1	2.8
Isopod	2	9.1	0	0
Unidentified insect eggs	1	4.5	2	5.5
Total	22	100.0	36	100.0

^a Three individuals of *Epuraea terminata* also found on bagged androecious flowers of *T. sieberi* at this site.

flower contains 80–100 long, dark purple-red setose styles which secrete a slight mucilaginous exudate on the surface (Fig. 16C). Androecious flowers split into 5–7 irregular, flat lobes and contain 100–150 T-shaped stamens with loculi held on lateral arms (Figs. 18H, 39B, C). The pollen is only slightly cohesive. Androecious flower color may be either dark purple-red or greenish white internally. I was unable to detect any floral odor from *T. tau* flowers during either day or night.

A population of *Tambourissa tau* at Perrier Nature Reserve was observed for pollinators for a total of 10.8 hours. The only insect to visit the flowers with any regularity was *Scaevinus truncatus*, a cryptic, nocturnal folivorous weevil found to occur on most species of *Monimia* and *Tambourissa* in Mauritius and Réunion. *Scaevinus* normally feeds on the leaves of *T. tau*, but during the flowering season weevils were found feeding on buds and flowers, grazing on the stamens, styles, and receptacle lobes. Large numbers of pollen grains were found trapped among the insects' body hairs and scales. To test the weevil's vagility, marking experiments were carried out on *Scaevinus* at Perrier. Among 52 individuals of *T. tau* studied, 8–28% were found to harbor *Scaevinus* on a given day. Out of 27 *Scaevinus* marked at the onset of the experiment, 18 (67%) had moved to other plants in the same population after three days. As *T. tau* occurs at comparatively high population densities at Perrier

(57 plants/512 m², or an estimated 1,113/ha), with nearest neighbor distances averaging only 160 cm (Fig. 3B), and fruit set in the wild is relatively high, it appears that *Scaevinus* is effective in cross pollinating *T. tau*. Although *Scaevinus* was also seen feeding on flower buds of *T. peltata* at Perrier, it was never observed to visit its flowers, nor those of any other *Tambourissa* or *Monimia* species. Finally, no other insects were observed to visit the flowers of *T. tau*.

TAMBOURISSA CORDIFOLIA

A study of this species was carried out at Pétrin Nature Reserve where *Tambourissa cordifolia* is common and forms dense, local populations in a low, scrubby *Philippia* heath formation. It is a small, dioecious shrub 1–2 m high with erect, multiple stems bearing medium-sized solitary or fasciculate flowers on leafless nodes. The androecious flower splits into four flat, spreading-reflexed lobes with 300–400 white stamens (Figs. 20C, 42B), which release white, coalescent pollen. The hollow, obconic gynoecious receptacle is shallow and splits apically into four erect or outcurved deltoid lobes that are ribbed and whitish within (Fig. 42G, H). The floral entrance is 10–12 mm wide and allows access to 100–400 short, purple-red conical styles that produce a sparse surface secretion (Fig. 13E). Flowers of both sexes emit a strong, pleasantly fruity floral odor likened by various observers to that of ripe

TABLE 13. Summary of results of *Tambourissa* crosses carried out in Mauritius (1978–1979) and at the Missouri Botanical Garden (1980).

Species & Locality	No. ♀ Flowers Outcrossed	No. Fruits Devel- oped	% Fruit Set	No. ♀ Flowers Selfed	No. Fruits Devel- oped	% Fruit Set
<i>T. amplifolia</i> , Bel Ombre	8 (3 individuals)	1	12.5	8 (3 individuals)	0	0
<i>T. cordifolia</i> , Pétrin	4 (2 individuals)	3	75.0	(Dioecious)	—	—
<i>T. cordifolia</i> × <i>T. peltata</i> ,	8 (2 individuals)	1	12.5	—	—	—
<i>T. peltata</i> , Perrier	7 (2 individuals)	7	100.0	(Dioecious)	—	—
<i>T. peltata</i> × <i>T. cordifolia</i>	2 (1 individual)	2	100.0	—	—	—
<i>T. purpurea</i> , cultivated, St. Louis	—	—	—	15 (1 individual)	0	0
<i>T. quadrifida</i> , Yemen Valley	15 (3 individuals)	14	93.3	16 (3 individuals)	0	0
<i>T. sieberi</i> , Mt. Cocotte	2 (2 individuals)	2	100.0	11 (2 individuals)	4	36.4
<i>T. sieberi</i> × <i>T. tau</i>	2 (1 individual)	2	100.0	—	—	—
<i>T. tau</i> , Perrier	12 (8 individuals)	12	100.0	16 (8 individuals)	0	0

apricots, ripe stewed bananas, or ripe jackfruit, which is perceptible for several meters. The species is dioecious and therefore obligately outcrossing.

A mature flowering individual of each sex was selected for study totalling 23 hours of observation time (Table 11). Pollinator activity began at dawn (ca. 5:45 A.M.) as the dense mists dispersed. Numerous small dipterans then began congregating on both androecious and gynoe-cious flowers (up to 25 insects per flower; Fig. 20C) drawn by the strong, fruity odor. *Drosoph-ila nasuta* and *Zaprionus vittiger* were the most frequent visitors, with smaller numbers of *Ly-ciella* and *Homoneura* (both Lauxaniidae) (Table 11). The insects fed on the pollen of the androe-cious flowers and drank dew and possibly stylar exudate from the gynoe-cious flowers. Consid-erable interfloral and interplant movement oc-curred at this time. Insect activity began to abate after 7:00–8:00 A.M. with an increase in temper-ature and wind velocity and generally ceased completely by 9:00 or 10:00 A.M.

Pollen grains adhered to the bodies of all the insects examined, suggesting they are effective as pollen vectors, although no actual pollen counts were made. In addition, the population density of *Tambourissa cordifolia* was extremely high at Pétrin (69 individuals/410 m², or an estimated 1,684/ha), with a mean nearest neighbor distance of 78.5 cm (Fig. 3C). Over 50% of the individuals in this population were actually situated within 50 cm of each other (Fig. 3C).

Judging by the relatively high wild fruit set and good regeneration of *Tambourissa cordifolia* at Pétrin, ample cross pollination takes place. As

Drosophilidae breed in decaying fruit and fungi, and *Lauxaniidae* breed in decaying vegetation (Borror & Delong, 1971), it is likely that signif-icant pools of these insects are available during the plants' three to five month flowering period. Significantly, Thien (1980) also recorded two of the same dipteran genera (*Drosophila* and *Homoneura*) as pollinators of *Drimys* in New Guinea.

TAMBOURISSA AMPLIFOLIA

A slender treelet 6–8 m tall, *Tambourissa am-plifolia* is occasional to locally common in the understory of some lowland and lower montane wet forest areas in Mauritius. It is monoecious and basally cauliflorous. Flowering takes place from November through January and up to 24 long-pedicellate flowers are open at a given time, each lasting for 10–15 days.

The white androecious flowers split into four flat lobes and resemble those of *Tambourissa cordifolia*, but are only half as large with 150–200 stamens (Fig. 18B). The shallowly napiform gynoe-cious flowers also resemble those of *T. cor-difolia*, but are half as large with four everted lobes, a broad orifice, and ca. 300 short, yellow or purple styles situated in the shallow, discoid receptacle. Only slight amounts of mucilage are secreted by the styles. Flowers of both sexes pro-duce a faint, fruity odor.

One individual of *Tambourissa amplifolia* was observed at Bel Ombre for a total of 4.5 hours during the morning (Table 11). Several drosophi-lids (*Drosophila* cf. *nasuta* and *Homoneura* sp.) repeatedly visited flowers of both sexes. Al-

TABLE 14. Contents of *Tambourissa quadrifida* gynoecious flowers sampled at Matala Valley (Yemen), Mauritius in March, June, and July 1979.

Contents	No. Flowers From Tree	% Total	No. Flowers Fallen From Ground	% Total
Empty	410	93.6	100	75.8
Mealybugs (Homoptera, probably Pseudococcidae)	1	0.2	15	11.4
Ants (Hymenoptera, Formicidae)	14	3.2	4	3.0
Silk webbing & pupa (probably Lepidoptera)	6	1.4	3	2.3
Silk webbing & larva (probably Lepidoptera)	2	0.5	2	1.5
Coleoptera, Nitidulidae, <i>Haptoncus luteolus</i>	1	0.2	—	—
Detritus (feces)	3	0.7	5	3.8
Empty egg cases	1	0.2	2	1.5
Springtail (Collembola)	—	—	1	0.7
Total	438	100.0	132	100.0

though visits were less extensive than in *T. cordifolia*, the same pollinator syndrome appears to be operative. Individuals of *T. amplifolia* are generally separated by distances less than 10 m, which the insects should be able to cross. Outcrossed flowers of *T. amplifolia* yielded a low fruit set (12.5%) although it is unclear why (Table 13).

TAMBOURISSA PELTATA

A medium-sized dioecious canopy tree, *Tambourissa peltata* is common and widespread in wet and cloud forests throughout the island. Flowering lasts from March to June and each individual generally has three to ten flowers open at a given time, although a large androecious plant may produce up to 58 open flowers during peak flowering. The exposed flowers are produced either singly or in groups of two to three on the older, leafless branches in the canopy and on the upper trunk, thus making pollination studies difficult. It is dioecious and obligately outcrossing.

The broad gynoecious receptacle splits open by four or five ornate, dark purple-red verrucose sterile lobes that spread flat, resembling a *Stapelia* flower (Figs. 15A, 17E). The flat gynoeceal disc is orange and bears ca. 400–500 flat, densely crowded columnar styles. At anthesis, the entire disc is covered by a layer of thick, sweet mucilage that functions both as a compitum and as nectar. Androecious flowers split gradually into four or

five ultimately reflexed lobes bearing 200–400 stamens that release abundant, coalescent pollen (Fig. 17D). Both salmon pink and dark purple-red androecious color morphs occur, according to the individual. Flowers of both sexes produce a strong, sour odor of rotting fruit or tomatoes and persist on the tree for 10–15 days.

The species was studied at Mare Longue Plateau and at Perrier and Pétrin Nature Reserves (Table 11) for a total of 8.2 hours and supplemented by additional insect collections. Most frequent visitors were Diptera, notably Syrphidae and Drosophilidae (Table 11). In the early morning, large numbers of *Drosophila* and *Zaprionus* congregated on both androecious and gynoecious flowers as in *Tambourissa cordifolia*, in addition to a few small Coleoptera (*Enicmosoma*, *Epuraea*). As the sun rose higher and the temperature increased, the drosophilids gradually left and were replaced by syrphids. The Syrphidae *Askarina* and *Ornida* were active throughout the day, periodically visiting different flowers on the same and on different trees. They often remained on flowers for extended periods to feed on the pollen (up to 43 minutes on a single flower for *Ornida obesa*), and also drank mucilage from the gynoecious flowers. Captured insects were found to have abundant pollen on their bodies. Other insect visitors included honeybees, which visited androecious flowers to gather pollen, but displayed no interest in the gynoecious flowers and their mucilage. The folivorous weevil, *Scaevinus truncatus*, while liv-

ing on *T. peltata* and feeding on its leaves and young flower buds, did not visit mature flowers and actually displayed an aversion to them, possibly repelled by the strong odor.

At Perrier, *Tambourissa peltata* occurred at comparatively low population densities of 26 individuals/12,700 m² (or an estimated 21/ha), with a mean nearest neighbor distance of 975 cm (Fig. 3A). Because of the relatively large distances separating individuals of this dioecious species, the strong-flying syrphids probably represent the most effective pollinators, although the role of drosophilids and small coleopterans as pollinators cannot be dismissed.

TAMBOURISSA FICUS

Tambourissa ficus is related to *T. peltata* but differs in being a small understory tree. It is usually subdioecious, producing one or two open flowers generally of a single sex at the swollen base of the trunk (Fig. 20E, F). Although only five to eight flowers are produced during the flowering season (Sept.–Dec.), they have the greatest dimensions of any in the family.

The urceolate-cupuliform gynoeceous flower has a broad orifice and is lined with ca. 1,000–2,000 long, yellowish pink setose styles which secrete small amounts of mucilage (Fig. 15C). Two androeceous floral forms occur, the first being cupuliform-urceolate like the gynoeceous flower, with erect lobes and white stamens (Fig. 20E). The other form splits open flat into five to seven ultimately reflexed lobes with pinkish purple stamens (Fig. 20F). The thick, apiculate stamens number 900–1,800 in both forms. Flowers of both sexes emit a fetid-aminoid, but slightly fruity, odor.

A tree with flat purple androeceous flowers at Brise Fer was observed for 0.8 hours at midday (Table 11). Male and female syrphids of the genus *Eumerus* were attracted to the flowers (Fig. 20F), and both captured insects had pollen adhering to their bodies. The cupuliform white androeceous flowers on a tree at Rivière des Galets (Fig. 20E) were visited by a different dipteran (unidentified). At Mt. Cocotte, however, large numbers of small Hydrophilidae beetles of the genus *Cercyon* were found in gynoeceous flowers and on open purple androeceous flowers on a single tree. Significantly, members of the same family also visited gynoeceous flowers of *Tambourissa sieberi* at the same locality, although

their role in the pollination of *T. ficus* is uncertain.

Although no crosses were carried out for *Tambourissa ficus*, it is probably at least partly outcrossing because of its tendency towards dioecy. Scattered individuals as well as denser local populations occur, and syrphids would seem to represent the most efficient pollinators, although the Coleoptera may also play a role. More extensive observations on the pollination biology of *T. ficus* are obviously required.

Flowers of *Tambourissa crassa* (Réunion) emit a strong, rancid-fruity odor and appear to display the same pollination syndrome as *T. ficus*. A gynoeceous individual of this dioecious species at Col de Bellevue (Lorence 2468, MO) was repeatedly visited by an unidentified dipteran which drank the mucilaginous secretion partly filling the mature gynoeceous flower (Fig. 20D).

MONIMIA OVALIFOLIA

A low, dioecious tree restricted to small patches of cloud forest on the island's highest mountains, *Monimia ovalifolia* is the only member of the genus to occur in Mauritius. Its numerous small flowers are produced in ramiflorous inflorescences from August to November. The globose gynoeceous receptacle takes on a pink to orange color at anthesis, but remains closed except for a small pore through which the six to 12 glistening white styles are exerted (Fig. 14B). These produce a slight surface secretion. The externally yellowish androeceous flowers split into four or five recurved valvate segments (Fig. 14A) much like those of *Tambourissa*. The numerous white stamens possess paired basal appendages (as in Fig. 13A) and release coalescent pollen. Flowers of both sexes produce a strong, sweet odor.

Androeceous and gynoeceous trees of *Monimia ovalifolia* were observed for 2.2 hours at Mt. Cocotte (Table 11). The flowers appear to be myophilous and were repeatedly visited by small, unidentified Syrphidae that licked the styles and fed on the pollen. They were found to carry *Monimia* pollen and could probably traverse the relatively short distances separating individuals of *Monimia* at Mt. Cocotte. It is therefore likely that syrphids are effective pollinators of *Monimia ovalifolia* in Mauritius.

DISCUSSION

Tambourissa species in Mauritius exhibit two different modes of pollination involving Coleop-

tera and Diptera, modes that occur in a number of other extant primitive angiosperms (e.g., Faegri & van der Pijl, 1971; Gottsberger, 1974; Thien, 1980). Thrips, which are known to visit flowers of other primitive angiosperms including Monimiaceae (Gottsberger, 1977), were not found in this study, although it is possible that they may visit some of the small flowered Comorean and Madagascan species of *Tambourissa*.

Flowers of *Tambourissa quadrifida* and *T. sieberi* seem to be primarily cantharophilous with the fruity odors, dull colors, and numerous floral parts (i.e., stamens and styles) characteristic of this syndrome (e.g., Faegri & van der Pijl, 1971). The inferior ovaries and abundance of receptacular idioblasts (see Morphology and Anatomy section) are probably also protective in this context. Gynoecious flowers of both species are further adapted for pollination by a variety of small, probably allotropic, Coleoptera and differ from the classic Magnoliaceous cantharophilous flower in the following ways: the flowers are long lived, apetalous, and remain permanently open. Furthermore, the gynoecious floral entrance is small, thus excluding many destructive predators, although larvae of the indigenous moth, *Opogona sacchari*, successfully feed on flowers and developing fruits of at least three species, including *T. sieberi* (Table 11). Both species produce only traces of mucilage on their styles and presumably deceive the insects by their strong, ripe fruity odors, although the long styles of *T. sieberi* may also be utilized as food bodies. Androecious flowers of all *Tambourissa* species offer only pollen as a reward, a resource taken advantage of by a variety of Diptera and the introduced *Apis*, as well as by the effective pollinators. Mass flowering of these species may compensate for pollinator inefficiency.

The drab, apparently odorless flowers of *Tambourissa tau* seem to represent a specialized cantharophilous syndrome adapted to pollination by a single insect, the folivorous curculionid, *Scaevinus truncatus*, which feeds specifically on Monimiaceae leaves. The flowers of this species represent a supplementary food source for *Scaevinus*, and *T. tau* has taken advantage of its presence for use as a readily available pollinator. The long styles represent a food source for the insect, while the basal stylar secretions presumably trap pollen grains from its body and legs. The peculiar T-shaped stamens with widely separated loculi may maximize pollen contact with *Scaevinus*, while also rendering the pollen load less liable to

be eaten at once. In any case, flowers of *T. tau* differ from the usual cantharophilous flowers and appear to be highly specialized. The energetic aspects of this relationship (cf. Heinrich & Raven, 1972) should prove to be most interesting.

The predominantly myophilous flowers of *Tambourissa amplifolia*, *T. cordifolia*, *T. ficus*, and *T. peltata* share a number of cantharophilous features with those of *T. quadrifida* and *T. sieberi*, i.e., strong fruity or aminoid odors and drab colors (in *T. ficus* and *T. peltata*). In fact, the latter two species also attracted some Coleoptera (Table 11), which is perhaps suggestive of a shift from cantharophily to myophily in *Tambourissa*. A number of other trends in these species suggest adaptations to allotropic fly pollinators (cf. Faegri & van der Pijl, 1971), including: paler floral colors (white androecious and pale yellow or pink gynoecious flowers in *T. cordifolia* and *T. amplifolia*, with white and salmon pink morphs occurring in androecious flowers of *T. ficus* and *T. peltata*, respectively), apically confluent anther loculi presenting the pollen more effectively (*T. amplifolia*, *T. cordifolia*, *T. peltata*); shallower and broader gynoecious receptacles with a larger entrance (extreme in the flat, discoid flowers of *T. peltata*), surrounded by attractive, spreading sterile lobes that act as landing platforms; more copious, sweet mucilaginous exudate with a nectar function in the gynoecious flower (*T. peltata*, Figs. 15A, 17E); a shortening of the stamens and styles to accommodate the insects' short probosces.

Although certain common features occur in these species, there appear to be two distinct trends. The first is a "fruit fly" syndrome involving small drosophilids that occurs in *Tambourissa amplifolia* and *T. cordifolia*. These plants are small in stature, occur in comparatively dense populations, and have smaller and paler flowers with a sweet, fruity odor produced near the ground. Significantly, Thien (1980) recorded two of the same fly genera as pollinators of *Drimys* in New Guinea, suggesting that these insects may pollinate a greater number of extant primitive angiosperms than previously suspected.

The second trend involves larger and more vigorous flies, primarily syrphids (in *Tambourissa ficus* and *T. peltata*). These are larger, more widely dispersed forest trees with more massive, pinkish to purplish flowers that emit sour, rancid, or otherwise fetid-aminoid odors with fruity overtones. Flowers are produced on the leafless upper branches (*T. peltata*) or near the ground

(*T. ficus*) and are exposed for easy access by the insects. Although androecious flowers of *T. ficus* were visited by syrphids and another dipteran in two cases (Table 11), flowers of both sexes of another individual attracted numerous hydrophilid beetles (*Cercyon* sp.). Hydrophilids were also found in gynoeceous flowers of *T. sieberi* at this same site. A more thorough study of *T. ficus* is needed to detail its significant pollinators.

Monimia ovalifolia displays a number of myophilous features, namely, a sweet floral odor, yellow to pink or orange receptacles, shallow, permanently open white androecious flowers, well exposed stamens and styles. Its flowers are well adapted to the small, probably allotropic syrphids that visit them.

In summary, species of *Tambourissa* in Mauritius exhibit two different modes of pollination based on Coleoptera and Diptera, and each mode displays two distinct trends involving modifications in size, shape, color, and odor of the flower. Pollinator modes also appear to be related to demography and life forms. Pollinator specialization presumably contributes to reproductive isolation in simultaneously flowering sympatric species (e.g., *Tambourissa amplifolia* and *T. tau*). Another factor contributing to reproductive isolation between sympatric species is different flowering times, clearly operative in *Monimia* species in Réunion (see section on Habitat and Ecology), and also for Mauritian *Tambourissa* species with common pollinators (e.g., *T. ficus* flowers from September to December; *T. peltata* flowers from March to June). Reproductive isolation appears to be effective, as hybridization is extremely rare in the wild in Mauritius, although artificial crosses resulted in fruit set in three different interspecific combinations (Table 13).

Prolonged flowering periods and high floral output may compensate for low pollinator efficiency. Finally, dioecism and self-sterility in monoecious species can be viewed as representing mechanisms to enforce outcrossing (e.g., Bawa, 1974; Bawa & Opler, 1975). Self-compatibility in *Tambourissa sieberi* most likely offsets low population densities and low efficiency of its small pollinators.

SYSTEMATIC TREATMENT

MONIMIACEAE Jussieu, Ann. Mus. Natl. Hist. Nat. 14: 133. 1809 (sub Monimiées).

Evergreen trees or shrubs, rarely lianas, usually aromatic, frequently dioecious or monoecious,

sometimes hermaphroditic. Leaves simple, usually opposite and decussate, rarely ternate, alternate or anisophyllous, exstipulate, with laminar oil glands, the trichomes simple, fasciculate and/or stellate, the venation festooned brochidodromous, rarely craspedodromous, the margin entire or serrate to dentate with glandular teeth. Inflorescence cymose or thyrse, or the flowers fasciculate or solitary, either terminal, axillary, ramiflorous or cauliflorous, the bracteoles small and caducous; flowers small to large, actinomorphic, rarely oblique, bisexual, polygamous or unisexual, the receptacle $\pm$ well developed, globose, ovoid to obovoid, urceolate, napiform, campanulate or discoid, the tepals subequal, spiral, whorled or decussate, large and petaloid to small or $\pm$ lacking; androecious flowers with few to numerous stamens in 1-many series or irregularly disposed, the filaments usually short and flattened, occasionally with a pair of basal appendages, the anthers erect, (2-)4-sporangiate, the loculi separate or confluent apically or rarely basally, lateral or $\pm$ unifacial, valvate or longitudinally dehiscent; gynoeceous flowers with or without staminodes, the carpels several to numerous, rarely solitary, unilocular, shortly stalked or sessile, free or enclosed or immersed in the receptacle wall, the style short or elongated, the stigma terminal, dry or secreting mucilage, the ovule solitary, erect, horizontal or pendulous. Fruiting carpels exposed, or enclosed or immersed in the accrescent receptacle wall, indehiscent, often drupaceous with a membranous or fleshy mesocarp and/or aril-like appendage, or plumose (Atherospermoideae); endocarp membranous to bony, the seed erect to pendulous, the testa membranous, the endosperm abundant, oily and fleshy, the embryo straight, the cotyledons erect or divaricate.

The Monimiaceae sensu lato include the subfamilies Atherospermoideae, Hortonioideae, Siparunoideae, Monimioideae, and Mollinedioideae, and comprise some 30 genera and nearly 350 species in the tropics and subtropics, with the greatest diversity occurring in the southern hemisphere.

KEY TO GENERA OF MONIMIACEAE IN THE MALAGASY REGION

- 1a. Trichomes of leaf and stem in part or all stellate with 4-16 horizontal rays, the others simple or in fascicles of 2-4; abaxial laminar surface obscured by a dense, whitish indu-

ment of trichomes; stamens bearing a pair of appendages on filament (Monimioideae)

1. *Monimia*

- 1b. Trichomes of leaf and stem either simple or rarely in fascicles of 2–4, never stellate; abaxial laminar surface visible, not obscured by trichomes; stamens lacking appendages on filament (Mollinedioideae).

2a. Gynoeceous receptacle flat and discoid to $\pm$ concave, the carpels superior, subsessile to sessile, free on the disc, clavate to columnar; fruiting receptacle $\pm$ discoid, concave to convex, bearing the exposed, $\pm$ free drupes, not splitting at maturity.

3a. Buds and flowers with 7–15 large, thick obtuse tepals imbricate in 1–2 radial series; male floral receptacle unfolding gradually at anthesis, not splitting 2. *Decarydendron*

3b. Buds and flowers with 4–8(–16) small to minute decussate tepals; male floral receptacle splitting into 4 valvate segments at anthesis 3. *Ehippiandra*

2b. Gynoeceous receptacle $\pm$ urceolate, cupuliform to napiform, ellipsoid or cylindric (discoid in *T. peltata*), the carpels inferior, syncarpous, immersed in the receptacle wall; fruiting receptacle $\pm$ closed, the drupes immersed in the wall, splitting open irregularly at maturity

4. *Tambourissa*

Monimia Thouars, Hist. Vég. Iles France 35, tab. 9. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. ed. 1: 35, tab. 9. 1805; Willd., Sp. Pl. 4(2): 647. 1805; Juss., Ann. Mus. Natl. Hist. Nat. 14: 116. 1809; Poir., Encycl. Suppl. 3: 726. 1813; Spreng., Syst. 3: 906. 1826; Boj., Hortus Maurit. 289. 1837; Tul., Monogr. Monim. 307. 1855; A.DC., Prodr. 16(2): 661. 1868; Baill., Adansonia, Ser. 1, 9: 133. 1868–1870; Baill., Hist. Pl. ed. 2, 1: 299. 1871; Benth. & Hook., Gen. Pl. 3: 139. 1883; Baker, Fl. Mauritius 289. 1877; Hobein, Bot. Jahrb. Syst. 10: 56. 1889; Pax, Pflanzenfam. 3(2): 101. 1891; Cordem., Fl. Réunion 299. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901; Perk, Pflanzenr. 4, 101 (Nachtr.): 39. 1911; Vaughan, Mauritius Inst. Bull. 1: 76. 1937; Hutch., Gen. Fl. Pl. 1: 118. 1964. LECTOTYPE: *M. rotundifolia* Thouars, cf. Bullock, Kew Bull. 14: 44. 1960.

Dioecious pubescent aromatic evergreen trees, rarely shrubby; bud scales present. Leaves opposite, decussate, entire, strongly discolorous, the abaxial surface obscured by a dense indument of simple, fasciculate and/or stellate-peltate trichomes, the venation festooned brochidodromous. Inflorescence pubescent, a thyse or cyme,

rarely leafy, either ramiflorous, axillary or subfoliar on leafless nodes, rarely terminal, the bracts and bracteoles caducous, the flowers borne in umbelloid units of 2–7. Male receptacle pedicellate, obovoid or globose in bud, the apex with several pairs of minute, decussate tepals, splitting at anthesis into $4-6 \pm$ regular valvate segments, tomentose within, the short stamens numerous, multiseriate, the filament thin, subtended by a pair of basal appendages, the connective and filament reddish brown, full of oil cells, blunt or slightly prolonged and rounded, the anther ovoid, bilocular, the loculi separate, parallel, longitudinally dehiscent, introrse; pollen inaperturate, spheroid, spinose. Female receptacle pedicellate, globose-urceolate to ovoid-urceolate, the apex with several pairs of minute decussate tepals, the carpels 4–14 per flower, unilocular, subsessile, free, enclosed within the receptacle which is lined with dense, simple hairs, the styles simple, $\pm$ papillose, exerted through the narrow, 3–5-lobed orifice at anthesis, the ovule solitary, pendulous, anatropous. Ripe fruiting receptacle splitting into 3–5 irregular valvate lobes, pinkish red and partly velutinous within, exposing 4–12 ovoid-compressed fruiting carpels (drupes) surrounded by a fleshy orange mesocarp, the apical half covered by a fleshy orange styler aril, the endocarp whitish, thick, bony, mucronate, and longitudinally crested, the surface foveate, foveate-reticulate to foveate-sulcate.

Distribution. *Monimia* consists of three species endemic to the Mascarene Islands of Mauritius and Réunion. The presence of *Monimia* in Rodrigues is doubtful and based on a single collection of *M. ovalifolia* (Balfour s.n., K). As Balfour failed to mention the genus in his comprehensive work on the botany of Rodrigues (1879), I suspect the specimen is wrongly labelled and may actually have come from Réunion where Balfour also collected. The Balfour s.n. collection most closely resembles plants of *M. ovalifolia* from Réunion characterized by orbiculate leaves. Furthermore, Rodrigues does not even attain the minimum altitude at which the species occurs in Mauritius and Réunion.

TAXONOMIC HISTORY OF *MONIMIA*

Monimia was described by A. Du Petit-Thouars in 1804 based on two species, *M. ovalifolia* and *M. rotundifolia*, which he collected in Mauritius and Réunion respectively. Du Petit-Thouars described the genus accurately and not-

ed the close similarity between the androecious flowers of *Monimia* and those of *Tambourissa* (as *Ambora* Juss., and *Mithridatea* Comm. ex Schreb.). As *Monimia* differed from the latter most conspicuously in the structure of its gynoeceous flowers, he named it after Monima, wife of Mithridates.

In 1809, Jussieu created a new family (as Monimieae) for *Monimia*, *Tambourissa* (as *Ambora*), and four other genera of Monimiaceae, which were all previously placed in the Urticaceae by various authors. Willdenow (1805) and Sprengel (1826) placed *Monimia* in subgroups of their "Dioecia," along with other anomalous genera belonging to unrelated families, but followed Du Petit-Thouars in noting its affinities to *Tambourissa*.

In his monograph of the family, Tulasne (1855b) placed *Tambourissa* and *Monimia* in separate tribes. *Monimia* was included in his "Drupaceae" (Monimieae) together with *Siparuna* Aubl. (as *Citrosma* Ruiz & Pav.), *Mollinedia* Ruiz & Pav., *Kibara* Endl., *Hedycarya* Forst., and *Peumus* Mol. (as *Boldea* Juss.) on the basis of their free, drupaceous carpels. Tulasne (1855b) also described an additional species of *Monimia*, *M. citrina*, which I consider to be synonymous with *M. rotundifolia*. Baillon (1868–1870, 1871) generally followed Tulasne, including *Monimia* under his "*Hortonia* series" (Hortonieae) with many of the same genera as Tulasne, although he included a number of others also having free, drupaceous carpels.

Bentham and Hooker (1883) recognized two large tribes of Monimiaceae on the basis of staminal dehiscence and position of the ovule. They placed *Monimia* with the bulk of genera now included in the Monimiaceae sensu stricto, a treatment largely followed by Hutchinson (1964).

Monimia has been placed in the tribe Monimieae within the subfamily Monimioideae, along with *Tambourissa*, *Palmeria* F. Muell., and *Hennecartia* Poisson by Pax (1891), Perkins and Gilg (1901), and Perkins (1911). Schodde (1970) created a separate subfamily for *Peumus* based on features of wood, pollen, and chromosome number but ignored *Monimia*, leaving it in the Monimioideae with the bulk of Monimiaceae sensu stricto. More recently, Thorne (1974) joined *Monimia* with *Peumus* as the sole members of the subfamily Monimioideae and created a new subfamily, the Mollinedioideae, to house the remaining genera formerly included in the Monimioideae.

SYSTEMATIC POSITION OF *MONIMIA*

Baillon (1871), Money et al. (1950), and Cavaco (1965) all noted floral morphological similarities between *Monimia* and *Palmeria*. In addition, the wood of *M. ovalifolia* and several species of *Palmeria* shows similar advanced trends (Garratt, 1934; Money et al., 1950). Other shared characters in *Monimia* and *Palmeria* include a dense indument of simple, fasciculate and stellate trichomes, an urceolate gynoeceous receptacle enclosing a small number of subsessile or sessile carpels, and a fruiting receptacle which splits open to reveal the ripe carpels set against a pink or red inner surface (Corner, 1976; Endress, 1980b). In spite of superficial similarities in the fruiting receptacles of the two genera, however, which may represent parallel lines of evolution, important differences also exist. The carpels of *Palmeria* are anatomically different from those of *Monimia* and possess a well-developed, hard and shiny black exocarp and thin mesocarp of starch-filled cells absent in the latter (Corner, 1976).

Monimia appears to have closer affinities with *Peumus*, a monotypic genus endemic to Chile. Both genera have horizontal axillary buds, stamens with paired appendages on the filaments, large, spinose pollen grains, the spines and surface composed of cable-like strands (smaller and spinulose in *Palmeria*), receptacles covered by a dense indument of simple, fasciculate and stellate trichomes, carpels with a fleshy mesocarp surrounding the bony white, sculptured endocarp (Fig. 19A, B), and also share the dioecious habit.

In *Peumus*, however, the stamens are tetrasporangiate and dehisce laterally, whereas in *Monimia* they are bisporangiate and dehiscence is nearly introrse along the inner margin (Fig. 13A). In these respects *Monimia* and *Peumus* appear to provide a link between the Atherospermoideae, with their bisporangiate anthers having valvate dehiscence and similar staminal appendages, and the Mollinedioideae, which have tetrasporangiate anthers with lateral dehiscence and lack staminal appendages (Sampson, 1969a, 1969b). As a result, the two genera do not fit satisfactorily into either subfamily.

Specialization in Monimiaceae is generally considered to be expressed in terms of floral simplification and reduction, both in terms of size and number of parts (Money et al., 1950; Endress, 1980b). In these respects, *Monimia* has attained a greater degree of floral morphological

specialization than *Peumus*, in spite of the latter's more specialized wood anatomy (Garratt, 1934; Money et al., 1950; Lemesle & Prichard, 1954). Although also dioecious, *Peumus* has retained a greater constellation of unspecialized floral characters, i.e., an elaborate perianth of whorled petaloid and sepaloid tepals, and a broad, shallow floral receptacle bearing exposed carpels in the manner of the putatively primitive *Hortonia* (Lemesle & Prichard, 1954; Endress, 1980a). Flowers of *Monimia* have reduced, scale-like decussate tepals, are closed in bud, and the female receptacle encloses the carpels—all advanced features.

Similarities which *Monimia* shares with *Peumus*, and to a lesser degree with *Palmeria*, suggest possible origin from a common ancestral stock. A *Monimia* precursor may have originally existed in Africa or Madagascar where it subsequently became extinct, but not before reaching the Mascarene Islands via long distance dispersal. The Mascarenes thus provided a refuge for *Monimia*.

Current work with sieve tube plastid analysis by Behnke (1977, and pers. comm.) has shown that *Palmeria* and *Peumus* possess fundamentally different types of sieve tube plastids (S-type and P-type, respectively). As *Monimia ovalifolia* possesses S-type plastids (Behnke, pers. comm.), this feature at least would seem to deny a close relationship to *Peumus*. Sieve element plastids unquestionably provide an additional taxonomically useful character when used in conjunction with other available data, but do not provide an adequate basis for fragmenting the Monimiaceae into some five families as proposed by Behnke (1981).

In summary, *Monimia* displays a number of advanced features, certain of which (i.e., its stamens) are transitional between the Mollinedioideae and the Atherospermoideae. As *Monimia* shares the greatest constellation of features with *Peumus*, however, the two genera are best placed together as constituting the Monimioideae as proposed by Thorne (1974).

KEY TO THE SPECIES OF *MONIMIA*

- 1a. Leaves amplexicaul with a deeply cordate base, sessile to subsessile; Réunion 1. *M. amplexicaulis*
- 1b. Leaves distinctly petiolate, the base neither deeply cordate nor amplexicaul; Réunion and Mauritius.
 - 2a. Stems, petioles and inflorescence hirsute-velutinous; trichomes on adaxial surface of lamina mixed simple, fasciculate and stellate with free, $\pm$ ascending arms; Réunion 2. *M. rotundifolia*
 - 2b. Stems, petioles and inflorescence at most scabrous or scurfy, not velutinous; trichomes on adaxial surface of lamina uniformly stellate-peltate with horizontal arms united basally for $\frac{1}{3}$ – $\frac{1}{2}$ their length; Réunion and Mauritius 3. *M. ovalifolia*

1. *Monimia amplexicaulis* Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 294, pl. 1, fig. 1a. 1982. TYPE: Réunion. Hauts du Tévelave: forestry road along the Domanial line, cloud forest transitional to heath formation, ca. 1,700 m, 6 Mar. 1979 (fl, fr), Lorence 2504 (holotype, MO; isotypes, K, MAU, P, REU, Z).

Shrub or small tree attaining 10 m tall and 30 cm diam., the bark grayish brown, longitudinally fissured, the new growth pale grayish to fulvous, velutinous-tomentose with predominantly short-armed stellate trichomes, mixed with long simple and fasciculate trichomes 0.5–1 mm long, the mature leafy stems 3–5 mm diam., velutinous-tomentose. Leaves opposite, sessile to subsessile; petiole stout, 3–5 mm long by 3–5 mm diam., velutinous-tomentose; lamina subcoriaceous to coriaceous, ovate to broadly ovate, broadly elliptic to suborbiculate, (40–)60–130 mm by (32–)40–110 mm, the apex shortly acute, shortly acuminate, mucronate or rounded, the base deeply cordate, amplexicaul, the secondary veins (4–)5–7 pairs, making a 40–60° angle with the costa, the venation depressed adaxially, visible to 3°, prominent and raised abaxially, visible to 4°, the adaxial laminar surface pubescent with predominantly stellate trichomes with 4–12 short horizontal arms, mixed with varying proportions of long simple and fasciculate trichomes with 2–4 ascendant arms, eventually glabrescent and $\pm$ pustular, glandular, the abaxial surface obscured by a dense whitish to pale yellowish indument of the same trichomes, the margin entire, pubescent, plane to slightly revolute. Inflorescence a congested, fulvous velutinous-tomentose thyrs or rarely short cyme of (3–)7–37 flowers (gynoeceous inflorescence more congested than the androecious), branching to 2°(–3°), leafy or not, ramiflorous or subfoliar on leafless nodes (the primary axis often continuing to grow as a leafy stem), axillary or rarely terminal, the floral axis (5–)10–60(–75) mm by 2–3 mm, often subtended by 1–several pairs of caducous, brown ciliate-pubescent naviculate bracts to 7 mm by 3 mm,

the peduncle 4–12 mm long, bearing an umbeloid unit of (2–)3(–6) flowers, occasionally subtended by a caducous, velutinous bracteole to 2 mm long or by a small leaf. Androecious flower in bud ellipsoid to obovoid, 2–7 mm long by 3–5.5 mm diam., velutinous-tomentose, the pedicel 3–7 mm by 1–1.5 mm, often subtended by 1–2 minute subulate bracteoles; at anthesis deeply 3–6-fid, 10–13 mm diam., the lobes ultimately reflexing; stamens (40–)60–150, 1.5–2.5 mm long, the anthers ellipsoid, ca. 1 mm wide, occupying ca. $\frac{1}{3}$ – $\frac{1}{2}$ total length of the stamen, the connective slightly prolonged and rounded, the internal receptacle surface tomentose, the simple hairs 0.3–0.8 mm long. Gynoecious flower in bud globose-urceolate to ovoid-urceolate, 4–5 mm long by 3–4 mm diam., at anthesis the orifice 0.8–1.2 mm diam., the styles 5–10, exserted for 1–2 mm, the internal receptacle surface velutinous with simple hairs 0.5–1.5 mm long, the pedicel 1.5–2.5 mm by 1–1.5 mm. Fruiting receptacles in clusters of 1–10 on the leafless branches, ovoid to subglobose, 7–15 mm diam., externally pubescent with stellate, fasciculate and simple trichomes, the carpels 1–10 per receptacle, ovoid to ellipsoid, 5–7 mm long by 3–5 mm thick, mucronate, with a longitudinal crest, the endocarp deeply foveate-reticulate. Figure 21.

Distribution. Endemic to Réunion (Fig. 22).

Habitat. *Monimia amplexicaulis* is occasional to abundant locally as a component of mid to upper level cloud forest and lower limits of the *Philippia* heath formations from ca. 1,400 to 2,100 m. It is most frequent on the sheltered, leeward escarpments of the “cirques,” e.g., at Petit Matarum, Coteau Kerveguen above Cilaos, Hauts du Tévelave, etc.

RÉUNION. CIRQUE DE CILAOS: ascent to Col de Taibit, 22 Mar. 1974 (fr), *Bosser 21677* (P); Plaine des Fraises, below Col de Taibit, 1,900 m, 2 Feb. 1967 (fl), *Cadet 663 bis* (REU); Cilaos to Col de Taibit, 1,950 m, 22 Mar. 1974 (fr), *Coode 2558B* (K); Montée Cilaos, Coteau Kerveguen, Feb. 1971 (fl, fr), *Bosser 20752* (P); path to Coteau Kerveguen, 1,500 m, 16 Nov. 1973 (fr), *Cadet 4512* (REU); Coteau Kerveguen, 1,500–1,700 m, 24 Feb. 1979 (fl), *Lorence & Rolland 2443* (MAU, MO); (fl), *Lorence & Rolland 2444* (MAU, MO); forest of Mare à Joseph, 1,400 m, 10 Jan. 1967 (fl), *Cadet 663* (REU); 1,200–2,000 m, Aug. 1943 (fl), *Rivals s.n.* (TL-R); 2,000 m, 11 June 1943 (fr), *Rivals s.n.* (TL-R); wet forest at Petit Matarum, 2,000 m, 22 Feb. 1975 (fl, fr), *Cadet 5049* (REU); (fl), *Cadet 5050* (REU); 4 Feb. 1968 (fl), *Capuron 28210-SF* (P); 6 Mar. 1971 (fl), *Friedmann 1118* (P); (fr), *Friedmann 1119* (P); path to Piton des Neiges, 15 Apr. 1978 (fl, fr), *Bosser 22498* (P); 28 Mar. 1973 (fr), *Lorence sub MAU 15693*

(MAU); (fl, fr), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Col de Fourche, 1,800 m, 29 May 1976 (fr), *Cadet 5435* (REU); valley of Bras Bémale, 1,500 m, 13 May 1976 (st), *Cadet 5404* (REU); above Belier, on Sentier des Scouts to Aurère, 1,500 m, 14 May 1976 (st), *Richardson 4132* (K). PLAINE DES CAFRES: base of Piton Bleu, 1,500 m, 11 July 1943 (fl), *Rivals s.n.* (TL-R); (fr), *Rivals s.n.* (TL-R); 24 Feb. 1945 (fr), *Rivals s.n.* (TL-R); path to Coteau Maigre, 2,100 m, Feb. 1971 (fl), *Bosser 20475* (P). PLAINE DES CHICOTS: 1,900 m, 19 Feb. 1945 (fr), *Rivals s.n.* (TL-R). PLAINE DES MERLES: Cirque de Salazie near La Nouvelle (sic), 1,300 m, 17 Feb. 1944 (fl), *Rivals s.n.* (TL-R). PLAINE DES SALAZES: Sources Bras Cabot, 17 Aug. 1944 (st), *Rivals s.n.* (TL-R). PLAINE DES TAMARINS: 20 Aug. 1944 (st), *Rivals s.n.* (TL-R). HAUTS DU TÉVELAVE: 1,700 m, 21 Sept. 1974 (fr), *Cadet 4797* (REU); (fl), *Cadet 4797 bis* (REU); along the Domanial line, 1,700 m, 6 Mar. 1979 (st), *Lorence 2501* (MO); (fl), *Lorence 2502* (MAU, MO); (fl, fr), *Lorence 2503* (MAU, MO).

Monimia amplexicaulis shares morphological features with *M. rotundifolia*, including the presence of three types of foliar trichomes (stellate, fasciculate, and simple; Fig. 9A). In *M. amplexicaulis*, the trichomes are predominantly stellate with short arms and not predominantly long, fasciculate and simple as in *M. rotundifolia*. *Monimia amplexicaulis* further differs from the latter by its sessile, deeply cordate, and amplexicaul leaves with 5–7 secondary veins and generally occurs at somewhat higher elevations in more sheltered habitats than *M. rotundifolia*, often at the cloud forest/heath formation interface.

Vernacular names. Mapou, Mapou des hauts (Réunion).

2. *Monimia rotundifolia* Thouars, Hist. Vég. Iles France 35, tab. 9, fig. 2. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. 21, 34, tab. 7, fig. 2. 1805; Willd., Sp. Pl. 4(2): 647. 1805; Spreng., Syst. 3: 906. 1826; Poir., Encycl., Suppl. 3: 727. 1843; Tul., Ann. Sci. Nat. (Paris) 4(3): 32. 1855; Tul., Monogr. Monim. 310, tab. 29a–j. 1855; A.DC., Prodr. 16(2): 661. 1868; Cordem., Fl. Réunion 299. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 66, fig. 18A–D. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911 (excluding *Balfour s.n.* collection from Rodrigues); Perk., Gatt. Monim. fig. 34A–D. 1925. TYPE: Ile Bourbon (Réunion). Without precise locality (ca. 1800–1801), *Petit-Thouars s.n.* (holotype, P).

Ambora tomentosa Bory, Voy. Iles Afrique 1: 317, tab. 13. 1804. *Myrtus villosa* Spreng., Syst. 2: 487.

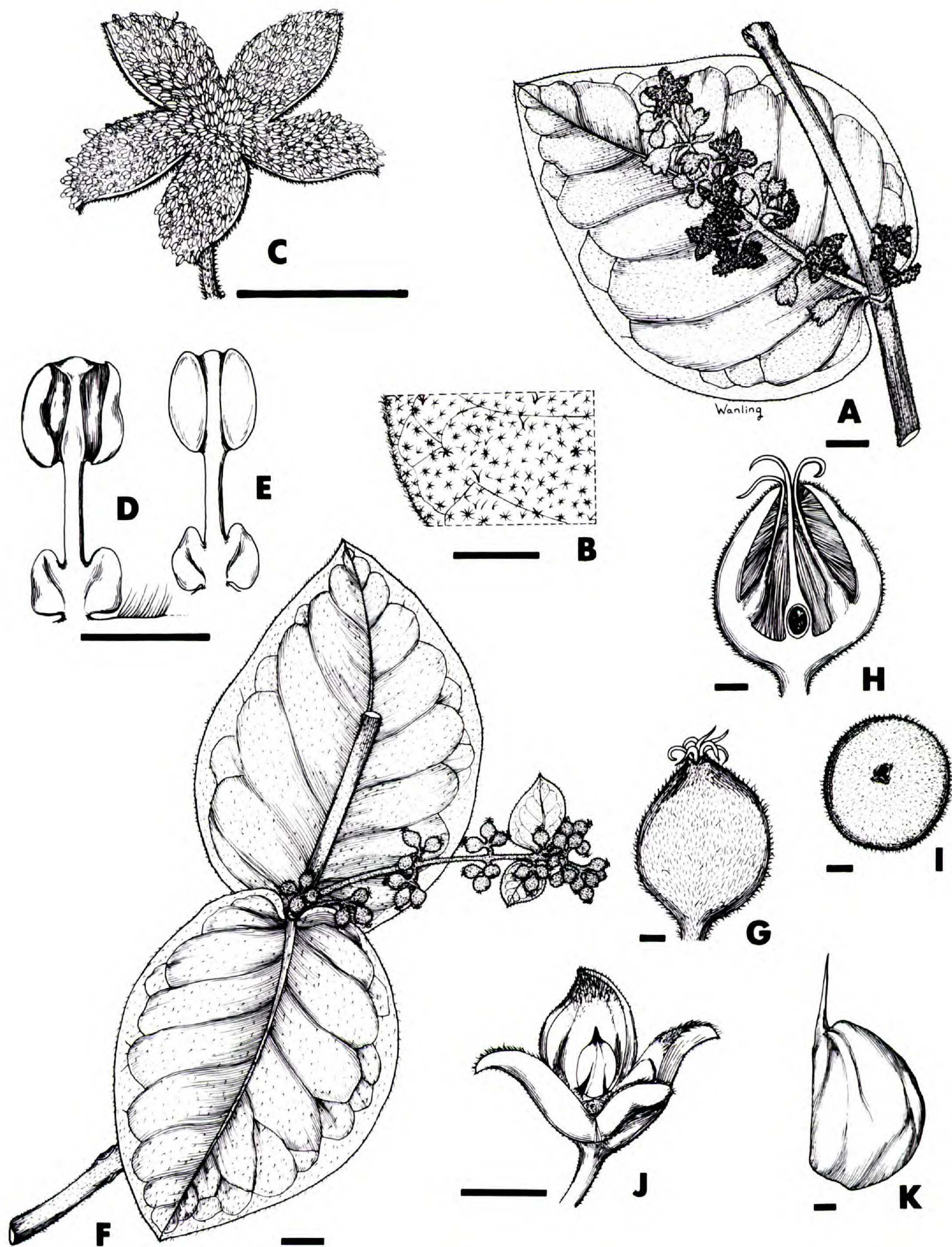


FIGURE 21. *Monimia amplexicaulis* Lorence. —A. Habit, male, one leaf removed. —B. Detail of adaxial leaf surface. —C. Androecious flower at anthesis. —D. Stamen, adaxial view. —E. Stamen, abaxial view. —F. Habit, female. —G. Gynoecious flower at anthesis, lateral view. —H. Gynoecious flower at anthesis, longitudinal section. —I. Gynoecious flower, apical view to show pore (styles removed). —J. Ripe fruiting receptacle, dehiscent. —K. Fruiting carpel, lateral view. A–E. Lorence 2444 (MO). F, J, K, Lorence 2404 (MO). G–I. Lorence 2503 (MO). Bars equal 10 mm in A–C, F, J, and 1 mm in D, E, G–I, K.

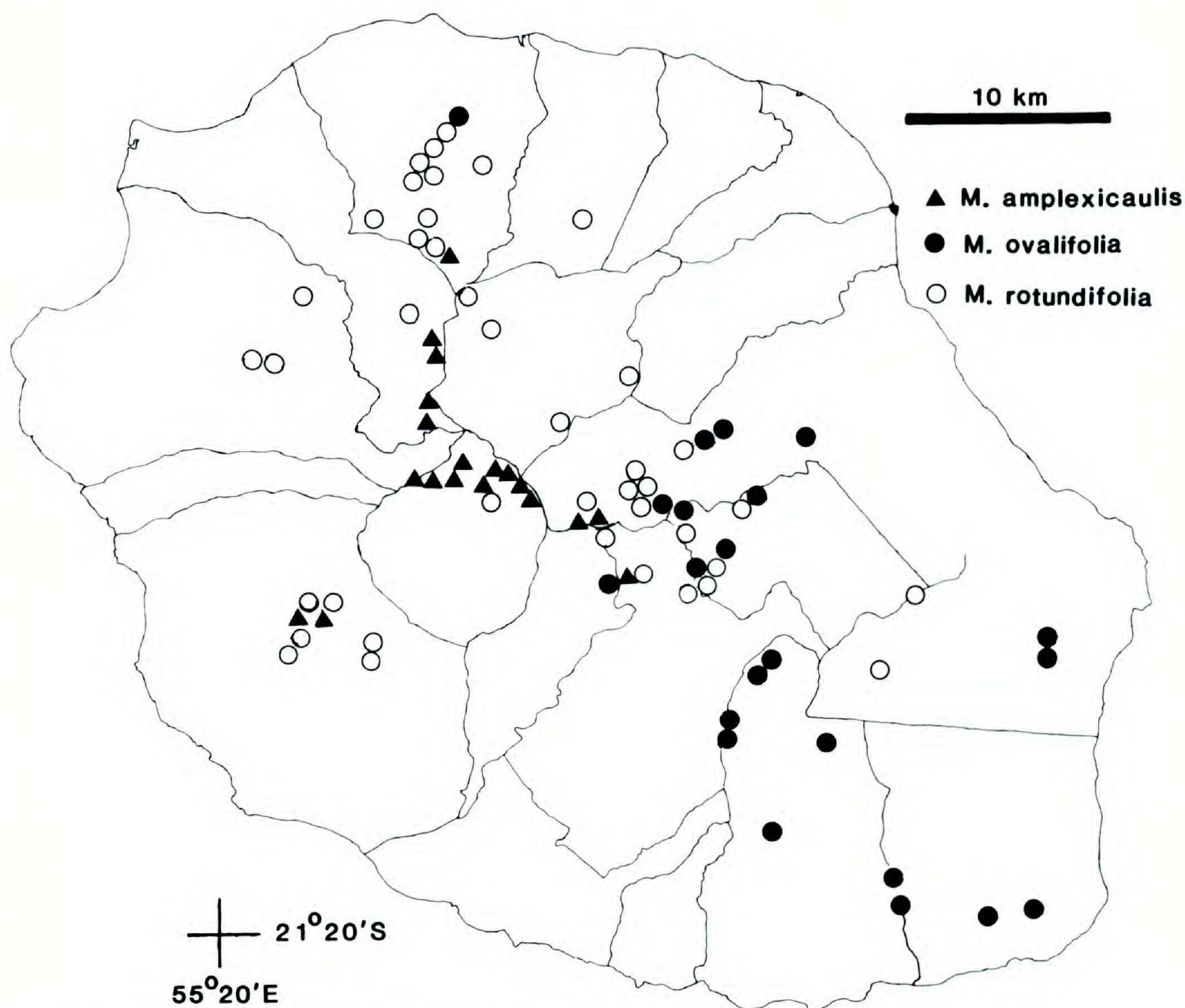


FIGURE 22. Distribution map of *Monimia* in Réunion.

1825, nom. superfl., based on type of *Ambora tomentosa* Bory. *Eugenia villosa* (Spreng.) Poir., Encycl., Suppl. 3: 124. 1843, nom. superfl. TYPE: without precise locality (probably Réunion), *Bory de St. Vincent* s.n. in 1821 (holotype, G-DC, n.v.; microfiche, MO).

Monimia citrina Tul., Ann. Sci. Nat. (Paris) 4(3): 32. 1855; Tul., Monogr. Monim. 311. 1855; A.DC., Prodr. 16(2): 661. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. TYPE: Ile de Bourbon (Réunion): without precise locality, *Gaudichaud* s.n. in 1836–1837 (lectotype, P, here designated; isoelectotype, P).

M. ovalifolia sensu Cordem., Fl. Réunion 300. 1895 non Thouars.

Shrub or low tree attaining 10 m tall and 60 cm diam., the new growth velutinous-tomentose, pale gray to fulvous, the simple and fasciculate trichomes 0.5–1 mm long, mixed with short stellate trichomes, the mature leafy stems 3–6 mm diam., velutinous-tomentose. Leaves petiolate; petioles 5–20 mm by 2–4 mm, velutinous-to-

mentose; lamina coriaceous, ovate to broadly ovate, elliptic to broadly elliptic or orbiculate, (35–)45–150 mm by (23–)35–160 mm (attaining 320 mm by 300 mm on vigorous sucker shoots), the apex shortly acuminate, acute, mucronate, obtuse, rounded or rarely retuse, the base acutely decurrent, acutely cuneate, obtuse, rounded or shallowly cordate, the secondary veins 3–7 pairs, making a 45–60° angle with the costa, the venation depressed adaxially, visible to 3°, abaxially raised and visible to 4°, the adaxial laminar surface strigose-hirsute, generally with predominantly long, simple hairs and fasciculate trichomes with 2–4 long, ascendant arms, mixed with varying proportions of stellate trichomes with 4–12 shorter horizontal arms, the surface glandular, eventually ± pustular, the abaxial laminar surface obscured by a dense, whitish to pale yellowish indument of the same trichomes, the margin entire, pubescent, plane to slightly

revolute. Inflorescence a congested to lax thyse (rarely a short cyme) of (3-)6-76 flowers (the gynoeceous inflorescence more congested than the androeceous), branching to 2-3°, leafy or not, velutinous-tomentose, either ramiflorous, subfoliar on leafless nodes (the primary axis sometimes continuing to grow as a leafy shoot), or axillary, the floral axis (7-)15-90(-130) mm by 1.5-2.5 mm, often subtended by 1-4 pairs of brown, scale-like, pubescent or ciliate bracts to 10 mm by 4 mm, the secondary axes 2-25(-50) mm long, occasionally subtended by a single caducous brown bracteole 2-3 mm long, the peduncle 2-12 mm long, bearing an umbelloid unit of 2-6 flowers. Androeceous flower in bud ellipsoid, obovoid or subglobose, 4.5-8 mm by 3-5 mm, velutinous-tomentose, the pedicel 3-13 mm by 0.5-1 mm, often subtended by 1-2 minute bracteoles; at anthesis deeply 3-5-fid, 4-14 mm diam., the lobes ultimately reflexing; stamens (25-)50-105, 2-3.5 mm long, the anther 1-1.4 mm wide, ellipsoid, occupying $\frac{1}{4}$ - $\frac{1}{2}$ total length of the stamen, the connective $\pm$ thickened, blunt or slightly apiculate, the internal receptacle surface tomentose, the hairs simple. Gynoeceous flower in bud ovoid-urceolate to globose-urceolate, 3.5-5 mm by 2.5-4 mm; at anthesis the orifice 1-1.2 mm diam., the styles 5-10, exserted for 1-2 mm, the internal receptacle surface velutinous, the short hairs simple, the pedicel 1.5-5 mm by 1-1.5 mm. Fruiting receptacles borne in clusters of 1-20 on leafy or leafless branches, ovoid to subglobose, 6-14 mm diam., externally pubescent with simple, stellate and fasciculate trichomes, the carpels 1-8 per receptacle, ovoid, 6-8 mm long, 4-6 mm wide, 4-5 mm thick, mucronate with a longitudinal crest, the endocarp thick, the surface deeply foveate, foveate-reticulate or foveate-sulcate.

Distribution. Endemic to Réunion (Fig. 22).

Habitat. *Monimia rotundifolia* is an occasional to locally abundant component of the cloud forest zone, rarely ranging into the *Philippia* heath zone, from ca. 1,000 to 2,000 m.

RÉUNION. BELOUVE: Apr. 1956 (fr), *Bosser* 7586 (P); 1,500 m, Apr. 1956 (fr), *Bosser* 9354 (P). BOIS DE NÈFLES: 1,500 m, 17 Sept. 1974 (fl), *Cadet* 4787 (REU); (fl), *Cadet* 4788 (REU); (fl), *Cadet* 4789 (REU). BOUCAN-LAUNAY: woods above Boucan-Launay (fr), *Boivin* 1120 (P). BRETAGNE: above Bretagne, 1,000 m, July 1945 (fr), *Rivals* s.n. (TL-R). BRÛLÉ DE ST. DENIS: 1,300 m, May 1957 (fl), *Bosser* 11577 (P); 1,000 m, 22 Oct. 1973 (fr), *Bosser* 21332 (P, 2 sheets); near Mamode Camp, 1,200 m, 13 Apr. 1968 (fr), *Cadet*

1333 (REU); vicinity of Mamode Camp, at Plaine des Chicots, 31 Jan. 1968 (fr), *Capuron* 28161-SF (P, 2 sheets); St. Francois, St. Denis (fr), *Cordemoy* s.n. (TL-R); 1,000-1,200 m, Oct. 1956 (st), *Rivière* s.n. (P). BÉBOUR: Bébou Forest, 4,500 ft. (ca. 1,350 m), 17 Nov. 1967 (fl), *Barclay* 554 (K, MAU); Bébou Pass and Rivière des Marsouins, 1,350 m, 21 Oct. 1973 (fl), *Bernardi* 14530 (BM, G, P); Bébou Plateau, 1,200-1,300 m, June 1957 (fl), *Bosser* 11488 (P, 2 sheets); 1,300 m, 27 Nov. 1973 (fl), *Cadet* 4531 (REU); 26 Oct. 1974 (fl, fr), *Cadet* 5197A (REU); 29 May 1975 (fl), *Cadet* 5197B (REU); Bébou Peak, 1,700 m, 27 Nov. 1973 (fl), *Coode et al.* 4231 (K, 2 sheets; REU); (fl), *Coode et al.* 4235 (K); (fr), *Coode et al.* 4237 (K, REU); (fl), *Coode et al.* 4238 (K, 2 sheets; REU); 16 Dec. 1970 (fl, fr), *Friedmann* 875 (P); 1,400 m, Nov. 1972 (fl, fr), *Friedmann* 1982 (P); 1,300-1,600 m, 23 Feb. 1979 (fl), *Lorence* 2429 (MO); 1,300 m, 6 May 1976 (fl), *Richardson et al.* 4086 (K, MO); (fl), *Richardson et al.* 4087 (K, MO); (fl), *Richardson et al.* 4088 (K, 2 sheets; MO). CIRQUE DE CILAOS: Petit Matarum, 6 Mar. 1971 (fr), *Friedmann* 1119 (P); Cilaos at Matarum, 1,300 m, June 1943 (fl), *Rivals* s.n. (TL-R). CIRQUE DE MAFATE: Sentier des Scouts, crest above Ilet à Malheur, 1,200 m, May 1976 (fr), *Richardson et al.* 4138 (K, 2 sheets). CIRQUE DE SALAZIE: path from Grand Ilet to Roche Ecrite, 1,900 m, 15 Oct. 1974 (fl, fr), *Cadet* 4836 (REU); below Grand Ilet at Salazie, 1,600 m, 26 Sept. 1977 (fl), *Cadet* 5254 (REU); (fl), *Cadet* 5255 (REU); Terre Plate, 1,600 m, 7 Apr. 1976 (st), *Cadet* 5334 (REU). MAÏDO: road to Maïdo above Petit France, 1,200 m, 22 Feb. 1979 (fr), *Lorence & Cadet* 2413 (MAU, MO); Maïdo to Le Guillaum road, 1,550 m, 12 May 1976 (fr), *Richardson et al.* 4121 (K, MO); (fl), *Richardson et al.* 4122 (K). MASSIF DE LA FOURNAISE: below the shelter at Pas de Bellecombe, 2,000 m, 25 July 1962 (fl), *Cadet* 202 (REU). MORNE DE PATATES À DURAND: 1,200 m, Hauts du Bois de Nèfles à St. Denis, 11 Sept. 1976 (fl), *Cadet* 5242 (REU); (fl), *Cadet* 5243 (REU). PLAINE D'AFFOUCHE: June 1945 (fl), *Rivals* s.n. (TL-R). PLAINE DES CAFRES: open heathland, 5,200 ft. (ca. 1,700 m), 2 Aug. 1968 (fl), *Barclay* 471 (K, MAU); Sentier Coteau Maigre, Feb. 1971 (fl, fr), *Bosser* 20476 (P); Piton Mare a Bouc, 1,600 m, 7 Nov. 1966 (fl), *Cadet* 503 (P, REU); foot of Piton Lepervanche, 1,700 m, 26 Oct. 1974 (fl), *Cadet* 4859 (REU); Col de Bellevue, 30 Nov. 1974 (fl), *Friedmann* 781 (P); (fl), *Friedmann* 782 (P); Col de Bellevue, 1,600 m, 27 Feb. 1979 (fl, fr), *Lorence* 2471 (MAU, MO); (fl), *Lorence* 2472 (MAU, MO); (fl), *Lorence* 2473 (MAU, MO); (st), *Lorence* 2474 (MO); 17 July 1979 (fl, fr), *Lorence* 2773 (MO, Z); (fl), *Lorence* 2774 (K, MO, Z); (fl), *Lorence* 2775 (K, MAU, MO, Z); base of Piton Bleu, 11 June 1943 (st), *Rivals* s.n. (TL-R); Grande Montée, mid and upper parts, 12 June 1943 (fl), *Rivals* s.n. (TL-R); lower part of forest at La Grand Montée, 1,200 m (st), *Rivals* s.n. (TL-R); scrub and cloud forest, 1,700 m, 5 Nov. 1966 (fl), *Schlieben* 10859 (B, MAU); Grand Montée, 1,600 m, 28 May 1964 (fl), *Staub* sub MAU 11105 (MAU); Grand Montée, 4,500 ft. (ca. 1,500 m), 10 Oct. 1960 (fl), *Wiehe* sub MAU 1534 (MAU); 1,600 m, 27 Nov. 1964 (fl), *Wiehe* sub MAU 11479 (MAU, 2 sheets). PLAINE DES CHICOTS: Roche Ecrite, 1,700-2,277 m, 8 Jan. 1975 (fl), *Bernardi* 14936 (P); (fl), *Bernardi* 14943 (P); Roche Ecrite, moist forest, 1,300 m, 23 July 1961 (st), *St. John* 26527 (G, 2 sheets; K).

PLAINE DES MAKES: 1,100 m, June 1957 (fl), *Bosser 12216* (P); 1,400 m, 6 Apr. 1975 (st), *Cadet 5154* (REU). PLAINE DES PALMISTES: mountainous regions (fl), *Cordemoy s.n.* (TL-R); Petite Plaine above Plaine des Palmistes, 1,200 m, 25 Feb. 1979 (fr), *Lorence & Rolland 2453* (MO). PLAINE DES SALAZES: high altitude ericoid vegetation, Apr. 1957 (fr), *Alphonsine s.n.* (P). RIVIÈRE DE L'EST: far up the Rivière de l'Est, 1,750 m, Nov. 1976 (fl), *Cadet 5710* (REU); (fl), *Cadet 5711* (REU). RIVIÈRE DES REMPARTS: Roche Plate path, 6,500–6,700 ft. (ca. 2,100 m), 16 Nov. 1967 (fl), *Barclay 498* (K, MAU); ca. 5,400 ft. (ca. 1,700 m), 20 Nov. 1968 (fl, fr), *Barclay 1272* (K, MAU); Vallée de la Rivière des Remparts, 1,700 m, 20 Nov. 1968 (fl, fr), *Cadet 1727* (REU); 7 Mar. 1975 (fl), *Cadet 5103* (REU); (fr), *Cadet 5104* (REU); (fr), *Cadet 5105* (REU). SAINTE AGATHE: 19 July 1875 (fl), *De L'Isle 383* (K; P, 2 sheets). SAINTE MARIE: Hauts de Sainte Marie, 1,200 m, 18 Apr. 1976 (fl), *Cadet 5511* (REU). TAKAMAKA: 900 m, 10 Mar. 1979 (st), *Lorence & Rolland 2532* (MAU, MO). TÉVELAVE: Hauts du Tévelave, 1,500 m, 21 May 1975 (fr), *Bosser 22189* (P, 2 sheets); 1,300 m, 5 Sept. 1975 (fl), *Cadet 5255* (REU); ca. 1,500 m, 25 Nov. 1968 (fl), *Edgerley E4 sub MAU 13372* (MAU); May 1976 (fl), *Friedmann 2817* (P); forestry road above Tévelave, 1,300–1,400 m, 28 Feb. 1979 (fr), *Lorence 2477* (MAU, MO); 1,700 m, 6 Mar. 1979 (fl), *Lorence 2505* (MAU, MO); (fr), *Lorence 2506* (MAU, MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. ex Herb. Kopp s.n.* (P, 3 sheets); (fl), *Anon. ex Herb. Station Agronom. Réunion s.n.* (P, 2 sheets); (fl), *Armange 20* (P); (fr), *Balfour s.n.* (K); (fl), *Barthe s.n.* (P); (fr), *Boivin 1120* (G, 2 sheets; P, 2 sheets); (fl, fr), *Boivin s.n.* (G; P, 3 sheets); (fl), *Bory de St. Vincent s.n.* (G-DC, microfiche); (fl), *Commerson s.n.* (BM, G, P; syntypes of *M. citrina*); (fl), *Commerson s.n.* (P); (fl), *De L'Isle s.n.* (P); (fl), *Gaudichaud s.n.* (G, P; syntypes of *M. rotundifolia*); (fl, fr), *Gaudichaud s.n.* (K, P); (fl), *Gaudichaud s.n. in 1837* (G); (st), *Giraudy s.n. in 1847* (P); (fl), *Monssi (?) s.n. in 1833* (P); (fl, fr), *Potier s.n.* (P, 3 sheets); (fl), *Richard 2* (K); (fl, fr), *Richard s.n.* (P, 3 sheets); (fl, fr), *Richard 27* (P, 2 sheets). LOCALITY (ISLAND) UNKNOWN: (fl), *Anon. sub Herb. ORSTOM 4999* (MAD); (fl), *Anon. sub MAU 2993* (MAU).

Monimia rotundifolia is an extremely variable species as to size and shape of the lamina, although its leaves are never sessile to subsessile and deeply cordate-amplexicaul as in *M. amplexicaulis*. Composition of laminar trichomes is also a variable feature. Long simple hairs predominate on the adaxial leaf surface of many individuals (e.g., Fig. 9C), but in others large numbers of long fasciculate and shorter stellate trichomes are present (e.g., Fig. 9B), approaching the condition found in *M. amplexicaulis*. Bojer (1837), followed by Baker (1877), erroneously stated that *M. rotundifolia* occurred in Mauritius, but cited no collections, and no authentic specimens are known from Mauritius. Its wood is occasionally used for construction in Réunion and is said to be virtually incombustible.

Vernacular names. Mapou, Mapou à grandes feuilles, Mapou blanc, Mapou des hauts (Réunion).

3. *Monimia ovalifolia* Thouars, Hist. Vég. Iles France 35, tab. 9, fig. 1. 1804; Thouars, Hist. Vég. Iles Austral. Afriq. 21, 34, tab. 7, fig. 1. 1805; Willd., Sp. Pl. 648. 1805; Spreng., Syst. 3: 906. 1825; Bojer, Hortus Maurit. 289. 1837; Poir., Encycl., Suppl. 3: 727. 1843; Tul., Monogr. Monim. 309. 1855; A.DC., Prodr. 16(2): 661. 1868; Baker, Fl. Mauritius 289. 1877; Cordem., Fl. Réunion 300. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 65, fig. 18E–F. 1901; Perk., Gatt. Monim. fig. 34E–F. 1925; Vaughan, Mauritius Inst. Bull. 1: 76. 1937. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1800–1801), *Petit-Thouars s.n.* (lectotype, P, here designated; isolectotypes, P, 2 sheets).

M. ovalifolia var. *boryana* A.DC., Prodr. 16(2): 661. 1868. TYPE: without precise locality (probably Mauritius or Réunion) (ca. 1821), *Bory de St. Vincent s.n.* (holotype, G-DC, n.v.; microfiche, MO).

M. citrina sensu Cordem., Fl. Réunion 300. 1895 non Tul.

M. rotundifolia sensu Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911 non Thouars, as to *Balfour s.n.* collection from Rodrigues (K).

Shrub or small tree 7–15 m tall and 40 cm diam., the bark pale brown, smooth, flaking, the new growth scurfy-pubescent, the mature leafy stems scurfy to scabrous, glabrescent, 2.5–5 mm diam., the stems, petioles, costa, and inflorescence axes scabrous to scurfy with mostly small, appressed stellate-peltate trichomes with 8–16 short, horizontal arms, mixed with fewer simple hairs and fasciculate trichomes with 2–8 long, ascendant arms. Leaves opposite, petiolate; petioles (3–)5–25 mm by 2–4 mm; lamina subcoriaceous to coriaceous, ovate-elliptic, elliptic, broadly elliptic, suborbiculate or orbiculate, occasionally obovate, (30–)50–130(–170) mm by (20–)30–110(–153) mm (attaining 200 mm by 200 mm with petioles 35 mm long on vigorous sucker shoots), the apex shortly acuminate, shortly acute, obtuse, rounded or retuse, the base acutely decurrent, acute, obtuse, rounded or shallowly cordate, the secondary veins 4–7 pairs, making a 50–65° angle with the costa, the venation depressed adaxially and visible to 2(–3°), raised abaxially and visible to 3(–4°), the adaxial laminar surface scabrous with scattered, ± ap-

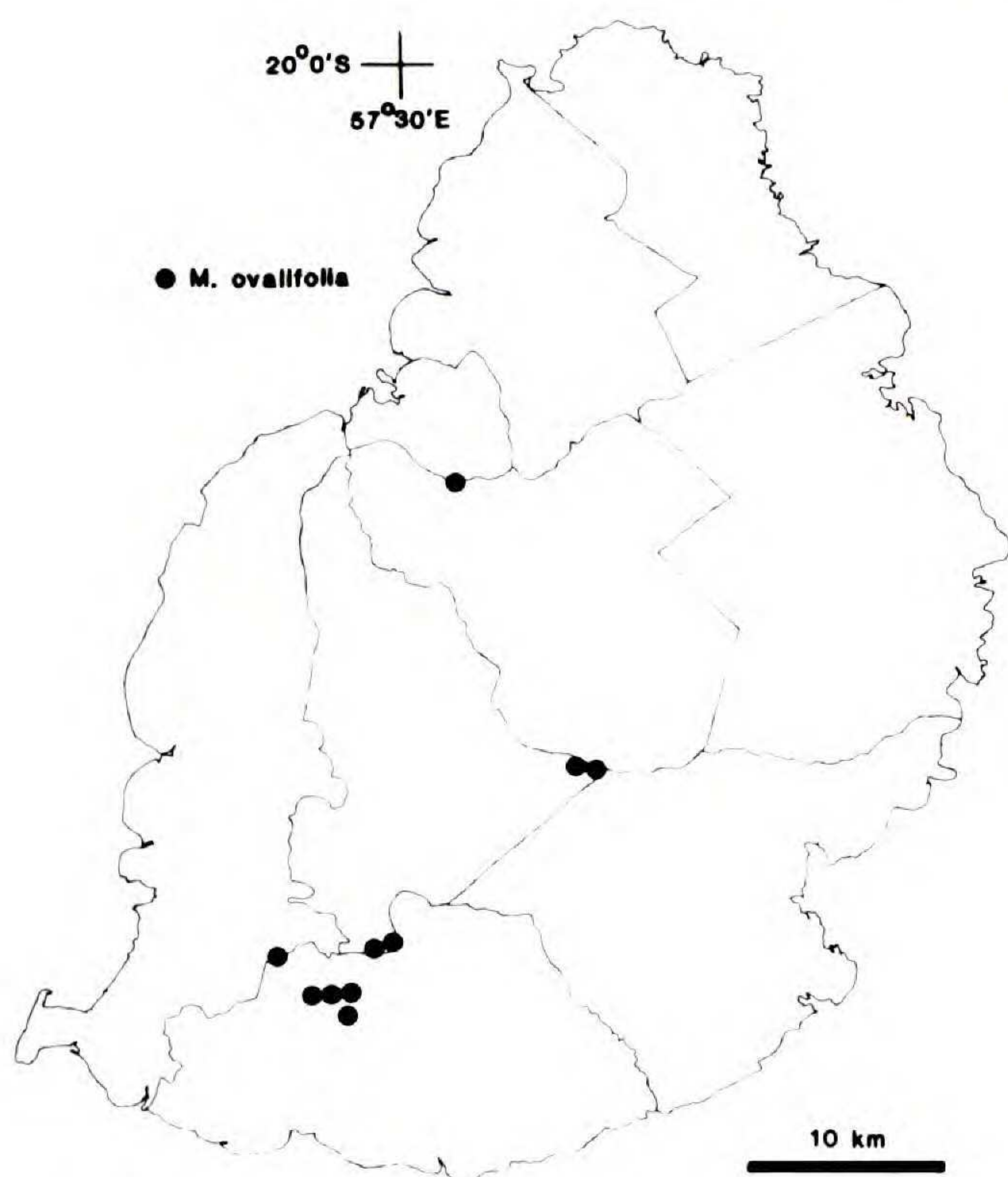


FIGURE 23. Distribution map of *Monimia* in Mauritius.

pressed stellate-peltate trichomes with 6–16 short, horizontal arms, the costa and secondary veins with scattered simple and fasciculate trichomes, eventually glabrescent and $\pm$ pustular, glandular, the abaxial laminar surface obscured by a dense whitish indument of the same trichomes, the margin entire, plane to slightly revolute. Inflorescence a scurfy to scabrous thyrses (rarely a short cyme or pleiochasium) of (3–)8–87 flowers, branching to 2(–3°), leafy or not, ramiflorous, either subfoliar on leafless nodes (the primary axis sometimes continuing to grow as a leafy stem), axillary, or rarely terminal, the floral axis (5–)10–120(–165) mm by 1.5–3 mm, often subtended by 1–several pairs of caducous brown, ciliate to pubescent naviculate bracts to 7 mm by 3 mm, the peduncle 3–20 mm by 0.5–1 mm, often subtended by a single caducous brown bracteole 2–5 mm long, or by a small leaf, bearing an umbelloid unit of (2–)3(–8) flowers. Androeious flower in bud ellipsoid to obovoid, 3–5 mm by 2.5–3 mm, the pedicel 1–7 mm by 0.3–0.6 mm, sometimes minutely bracteolate; at anthesis deeply 4–6-fid, 5–7 mm diam., the lobes reflexing; stamens ca. 45–60, 1.5–2 mm long, the anther ellipsoid, ca. 1 mm wide, comprising ca. $\frac{1}{3}$ – $\frac{1}{2}$ total length of the stamen, the connective rounded to apiculate, the internal receptacle surface pilose with short simple hairs. Gynoeious flower in bud ovoid-urceolate to subglobose-ur-

ceolate, 2.5–4 mm by 2.5–3.5 mm; at anthesis the orifice 0.6–0.8 mm diam., the styles 6–12, exserted for 0.5–1.5 mm, the internal receptacle surface velutinous with short simple hairs, the pedicel 1–4 mm by 0.5–1 mm. Fruiting receptacles borne on the leafy or leafless stems, in clusters of 1–20, ovoid to subglobose, 5–12 mm diam., the apex $\pm$ acuminate, externally scabrous with scattered stellate trichomes, the carpels 1–5 per receptacle, ovoid-compressed, 5–7 mm long, 4.5–5.5 mm wide, 3–4.5 mm thick, mucronate, with a longitudinal crest, the endocarp surface deeply foveate-sulcate.

Distribution. Endemic to the Mascarene Islands of Mauritius and Réunion (Figs. 22, 23).

Habitat. The species is occasional to locally common in lower montane wet and cloud forest in Réunion from ca. 500 to 1,700 m. In Mauritius, *Monimia ovalifolia* is known only from patches of cloud forest on the summits of Mts. Le Pouce, Cocotte, Lagrave, and Piton Grand Bassin (ca. 550–770 m), and also occurs in wet forest at Plaine Champagne (ca. 450 m).

MAURITIUS. BASSIN BLANC: path near Bassin Blanc, (fr), *Vaughan sub MAU 13081* (MAU). GRAND BASSIN: summit area, Piton Grand Bassin, ca. 700 m, 31 Jan. 1976 (fr), *Coode 4696* (K, 2 sheets); 18 Oct. 1978 (fl), *Lorence 1857* (MAU, MO); Chemin Cheval near Grand Bassin, 23 Jan. 1939 (fr), *Vaughan sub MAU 18546* (MAU). LE POUCE MT.: around summit, June 1860 (fl, fr), *Ayres s.n.* (K); at the upper limit of woods at the base of Mt. Pouce, 5 Sept. 1849 (fl), *Boivin s.n.* (P); (fl, fr), *Bojer s.n.* (K); base of the shoulder (fl), *Bouton s.n. in 1864–1865* (K); (fr), *Bouton s.n. in 1831* (P, 2 sheets); summit of the Pouce, highest part of the mountain (fl), *Bouton s.n.* (G-DC, n.v.; microfiche, MO); base of the shoulder (fl), *Bouton sub MAU 1307* (MAU); SE slope near the summit, 19 Nov. 1973 (fl), *Coode 4125* (K); ca. 30 m below summit on windward slope, 800 m, 14 Dec. 1978 (st), *Lorence 2145* (MO); 18 Aug. 1979 (fl), *Lorence 2910* (MO). MT. COCOTTE: mossy forest, summit, 10 June 1966 (fl), *Guého sub MAU 12175* (MAU, 2 sheets); indigenous vegetation along crest, 8 Nov. 1969 (fr), *Guého sub MAU 14130* (MAU, 2 sheets); summit, ca. 770 m, 1 Dec. 1978 (fl), *Lorence 1982* (K, MO); (fr), *Lorence 1983* (B, G, K, MAU, MO, P, REU, Z); 19 Dec. 1978 (st), *Lorence & Lecordier 2168* (MAU, MO, P); 17 Jan. 1979 (fr), *Lorence 2285* (MAU, MO); 29 Jan. 1979 (fr), *Lorence 2350* (MAU, MO); 10 Aug. 1979 (fl), *Lorence 2895* (MO); (fl), *Lorence 2896* (B, G, K, MAU, MO, P, REU, Z); 29 Jan. 1979 (st), *Lorence 2964* (MO). MT. LAGRAVE: dense thicket along crest, 27 Sept. 1969 (fl), *Guého sub MAU 14097* (MAU, 2 sheets); dense thicket on N flank, 27 Sept. 1969 (fl), *Guého sub MAU 14105* (MAU, 2 sheets); S slope facing Eau Bleue Reservoir, 620 m, 24 May 1979 (st), *Lorence & Lecordier 2650* (K, MAU, MO). PLAINE CHAMPAGNE: track from Plaine Champagne to Black River Gorges, 1,400 ft. (ca. 450 m), 4 Feb. 1975 (st),

Coode s.n. (K). WITHOUT PRECISE LOCALITY: (fl), *Ayres s.n.* (MO, 2 sheets); (fr), *Bijoux sub MAU 1308* (MAU); (fr), *Bijoux sub MAU 1309* (MAU); (fr), *Bijoux sub MAU 1310* (MAU); (fl), *Boivin s.n.* (P, 2 sheets); (fl), *Bojer s.n.* (K); (fl), *Bouton s.n. in 1829* (K); (fl), *Bouton s.n.* (P, 2 sheets); (fl), *Ilardwicke s.n.* (G); (fl), *Neraud s.n.* (G); (fl), *Schledl s.n.* (P); (fr), *Vesco s.n. in 1850* (P, 2 sheets). RÉUNION. BASSE VALLÉE: Le Grand Coudé (above St. Joseph), 1,100 m, June 1957 (fl), *Bosser 12215* (P); heights of Basse Vallée, La Coudée, 22 Nov. 1973 (st), *Coode s.n.* (K); ravine of Basse Vallée, 25 Nov. 1970 (fr), *Friedmann 753* (P); Basse Vallée near St. Philippe, 900 m, 13 July 1979 (fl), *Lorence & Cadet 2726* (MO); (fl), *Lorence & Cadet 2727* (MAU, MO); 17 May 1976 (st), *Richardson 4152* (K); 17 Feb. 1956 (st), *Severin 50* (P, REU). BOIS BLANC: above Bois Blanc, 800 m, 8 Aug. 1972 (fl), *Cadet 3721* (REU); 800 m, Apr. 1972 (fl), *Friedmann 1884* (P). BÉBOUR FOREST: Bébou Peak (Piton Rond de Bébou), 1,300–1,600 m, 23 Feb. 1979 (fr), *Lorence & Cadet 2430* (MAU, MO); region of Bébou near Pl. des Palmistes, 19 Jan. 1975 (fr), *Bernardi 15171* (P). GRAND ÉTANG: 500 m, 15 July 1979 (fl), *Lorence & Rolland 2754* (MO); (fl), *Lorence & Rolland 2755* (MAU, MO); (fl), *Lorence & Rolland 2756* (MAU, MO); (fl), *Lorence & Rolland 2757* (MAU, MO). LANGEVIN: high valley of Langevin, 1,500 m, 10 May 1976 (fl), *Cadet 5400* (REU); valley to Langevin below Plaine des Sables, 1,400 m, 10 May 1976 (fl, fr), *Richardson 4106* (K). MORNE DES PATATES À DURAND: 1,200 m, Mar. 1973 (fr), *Friedmann 2199* (P). PLAINE DES CAFRES: bank of Rivière des Remparts, 1948 (fl), *Anon. s.n.* (probably *Rivals*) (TL-R); Grand Bassin at base of Piton Bleu, 11–12 July 1943 (fr), *Rivals s.n.* (TL-R); Grand Montée of the Plaine des Cafres, 1,300–1,500 m, 12 July 1943 (fl), *Rivals s.n.* (TL-R); Bank of Rivière des Remparts, Vallon Hoarau, 20 Oct. 1948 (fl), *Rivals s.n.* (TL-R). PLAINE DES PALMISTES: high plateaux, (fl, fr), *Cordemoy s.n.* (TL-R); Grande Montée, 1,400 m, roadside, 20 Dec. 1942 (fl, fr), *Rivals s.n.* (TL-R); (fr), *Rivals s.n.* (TL-R); Petite Plaine above Plaine des Palmistes, 1,200 m, 25 Feb. 1979 (fr), *Lorence & Rolland 2452* (MAU, MO). RIVIÈRE DES REMPARTS: Roches Plates path, 5,400 ft. (ca. 1,800 m), 20 Nov. 1968 (fl), *Barclay 1273* (K, MAU); high valley of Rivière des Remparts, 1,700 m, 20 Nov. 1968 (fl), *Cadet 1726* (REU); 1,650 m, 7 Mar. 1975 (fl), *Cadet 5106* (REU). ST. PHILIPPE (VICINITY): Mare Longue forest, 500 m, 25 Feb. 1975 (fr), *Cadet 5082* (REU); 1–2 Feb. 1968 (fr), *Capuron 28182-SF* (P, 2 sheets); 23 Nov. 1973 (fr), *Coode et al. 4176* (K, 2 sheets; MAU, REU); 25 Feb. 1975 (fr), *Coode 4954* (K, 2 sheets; REU); 2 Mar. 1979 (fr), *Lorence, Lorence & Cadet 2482* (MAU, MO); Mare d'Arzule, 500 m, Apr. 1944 (fr), *Rivals s.n.* (TL-R). TAKAMAKA: path from Takamaka towards Ilet à Bananes, 2,500 ft. (ca. 800 m), 18 Feb. 1968 (fr), *Barclay 1240* (K, MAU); rain forest, Takamaka, 21 Dec. 1971 (fr), *Bosser 20926* (P); Takamaka forest, Ilet à Bananes, ca. 800–900 m, 10 Mar. 1979 (fr), *Lorence & Rolland 2531* (MO); ca. 1,000 m, 8 May 1976 (st), *Richardson et al. 4100* (K, MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. ex Herb. Ventenat s.n.* (G); (st), *Anon. s.n.* (probably *Cordemoy*) (TL-R); (fl), *Frappier 269* (P); (fr), *Frappier 270* (P); (fl), *Frappier 271* (P). LOCALITY (ISLAND) UNKNOWN: (fl), *Anon. ex Herb. Richard 66* (P); (fl), *Anon. ex Herb. Richard s.n.* (P); (st), *Anon. sub Herb. Willd. 18080* (B,

n.v.; microfiche, MO); "Madagascar" (probably Mauritius) (fl), *Colebrooke s.n.* (G); "Rodrigues" (probably Réunion) (fr), *Balfour s.n. in Aug.–Dec. 1874* (K).

Monimia ovalifolia differs from *M. amplexicaulis* and *M. rotundifolia* in having much sparser and uniquely short stellate-peltate laminar trichomes with the arms united basally for ca. $\frac{1}{3}$ – $\frac{1}{2}$ their length (Fig. 9D, E), flowers with much smaller receptacles, and in having tanniferous idioblasts in the petiolar cortex. Although characterized by a generally lower altitudinal range, *M. ovalifolia* occurs sympatrically with *M. rotundifolia* in many localities in Réunion (e.g., at Bébou), where both species remain distinct, apparently by temporal isolation of flowering.

Populations of *Monimia ovalifolia* from Réunion tend to have fewer simple and fasciculate trichomes on the stem, petiole, costa, and inflorescence. The leaves are larger than in Mauritius plants and more variable in shape, often obtuse or even orbiculate. Furthermore, crushed leaves of the Réunion plants usually produce a faint, citron-like odor not apparent in Mauritian plants, even though ethereal oil cells are present in the mesophyll of both. Intergradation of plants from the two islands is total, however, and formal recognition of infraspecific variants is impossible.

Vernacular name. Mapou (Réunion).

EXCLUDED SPECIES

Monimia lastelliana Baill., Bull. Mens. Soc. Linn. (Paris) 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. [= *Tambourissa lastelliana* (Baill.) Drake, see discussion under this species].

Decarydendron Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 279. 1928; Cavaco, Bull. Soc. Bot. France 105: 38. 1958; Cavaco, Blumea Suppl. 4: 28, fig. 1. 1958; Cavaco in Humbert, Fl. Madagascar 80: 8, fig. II:1–8. 1959. TYPE: *D. helenae* Danguy.

Monoecious treelets or small trees 4–8 m tall, the trunk sometimes swollen basally, the new growth velutinous to canescent, the hairs simple or in fascicles of 2. Leaves opposite, petiolate, adaxially glabrescent, abaxially $\pm$ pubescent especially along costa and major veins, the venation festooned brochidodromous, the margin serrate to dentate; juvenile and sucker leaves unknown. Inflorescence cauliflorous, sometimes produced at the swollen base of the trunk, or

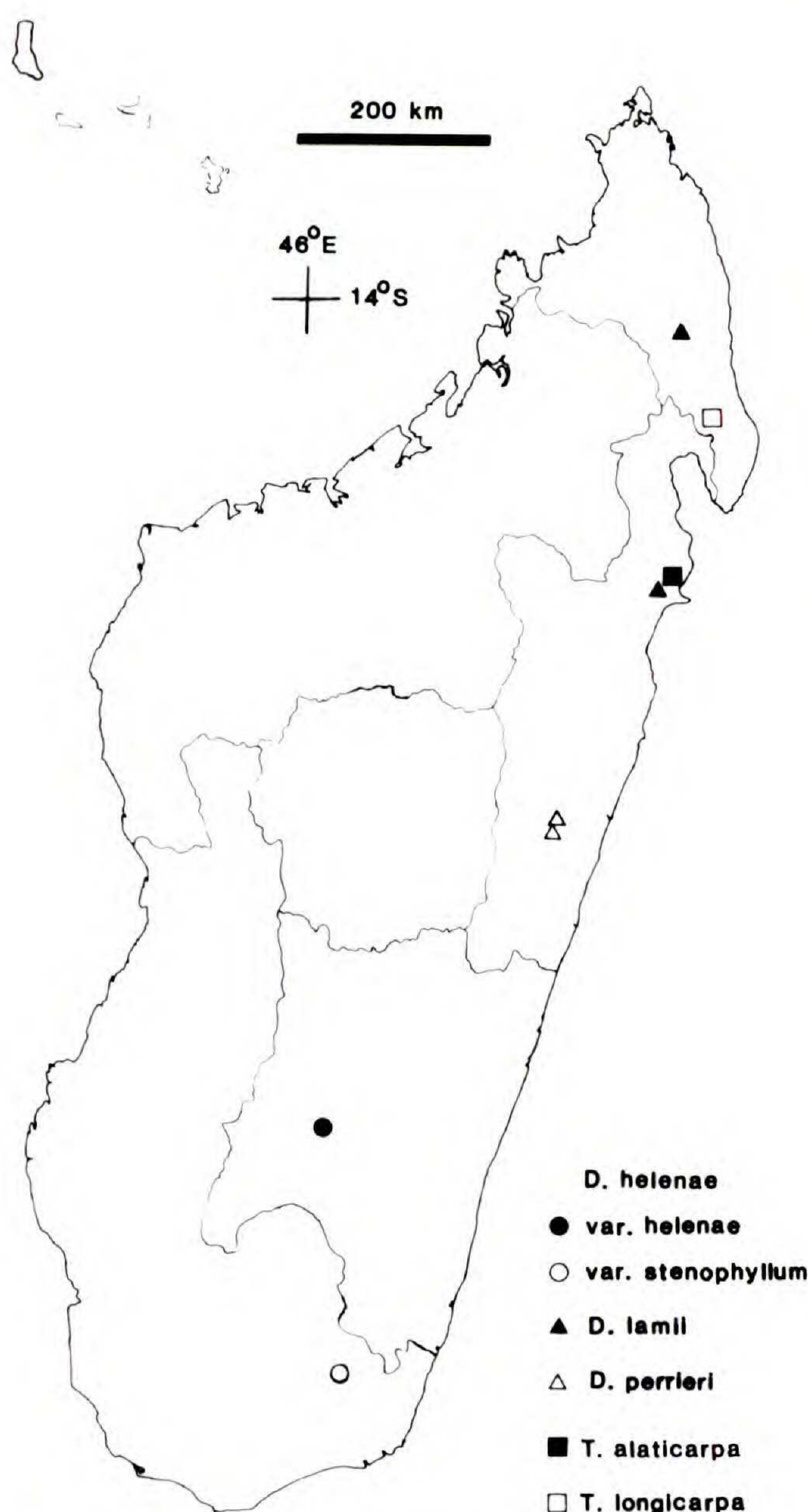


FIGURE 24. Distribution map of *Decarydendron* and two species of *Tambourissa* in Madagascar.

ramiflorous, a short, pubescent unisexual or sexually mixed pleiochasium of 5–15 flowers, often terminated by a gynoeceous flower, the pedicels short, bracteolate. Androeceous flower in bud subglobose to napiform, pubescent, the tepals imbricate, opening gradually, not splitting, at anthesis shallowly cupuliform to hemispherical, the rim bearing 10–15 large, subequal, broadly obtuse, radially arranged tepals in 1–2 series; stamens eglandular, 16–60, situated on the $\pm$ glabrous inner receptacle surface, the filament slender, distinct, the anther ovoid-ellipsoid, tetrasporangiate, the 2 loculi lateral, separate, longitudinally dehiscent, extrorse, the connective small, scarcely or not prolonged; pollen inaperturate, spheroid to subovoid, the sexine corrugate to rugulate, the sexinous elements short, finger-like. Gynoeceous floral receptacle subglobose

in bud, expanding gradually, not splitting, at anthesis broadly obconical to turbinate, $\pm$ angular, the walls fleshy, the rim bearing 9–15 broadly obtuse, radially arranged tepals, often eventually caducous, the carpels numerous, ca. 300–1,000, free, lining the receptacle, subsessile, clavate, ca. 1.5–2 mm long, $\pm$ polyhedral, the small stylar canal situated laterally in the basal half, the solitary ovary unilocular, the small loculus confined to the base of the carpel, containing a single pendulous, anatropous ovule, the carpels interspersed with $\pm$ dense, short simple hairs. Fruiting receptacle, mature carpels, and chromosome number unknown.

The genus was named after the French botanical explorer, R. Decary, who collected in Madagascar during the early part of the twentieth century.

Distribution. The three described species of *Decarydendron* are endemic to the wet evergreen forest zones of central and eastern Madagascar (Fig. 24).

TAXONOMIC HISTORY OF *DECARYDENDRON*

The genus *Decarydendron* was described by Danguy (1928) based on the species *D. helenae*. Thirty years later Cavaco (1958a, 1958b), described two additional species, *D. perrieri* and *D. lamii*, as well as another variety of *D. helenae*, var. *stenophyllum*, in preparation for his treatment for the “Flore de Madagascar” (1959). Herbarium material is scarce, and many additional flowering and fruiting collections and field observations are required for a meaningful revision of the genus.

SYSTEMATIC POSITION OF *DECARYDENDRON*

Decarydendron possesses the greatest constellation of primitive characters of any of the Malagasy Monimiaceae genera, notably the broad, shallowly concave floral receptacles with many large, whorled imbricate tepals, the numerous free, subsessile clavate carpels, and the cupuliform androeceous flowers which expand gradually without splitting into segments as in the other genera (Fig. 14E). These features readily distinguish *Decarydendron* from the other two Madagascan genera which form an increasingly specialized series. *Decarydendron* resembles *Hedycarya* from Oceania in a number of respects, including the gynoeceous floral morphology. Its mature fruiting receptacle presumably resembles

that of the latter genus in having numerous sessile carpels situated on a flat, discoid receptacle.

Money et al. (1950) placed *Decarydendron* in the subfamily Monimioideae with the other Madagascan genera. Hutchinson (1964) placed it in the tribe Hedycaryeae within the same subfamily on the basis of its free, sessile carpels. In redefining the Monimioideae to include only *Monimia* and *Peumus*, Thorne (1974) created a new subfamily, the Mollinedioideae, to house the remaining genera formerly included in the Monimioideae. *Decarydendron* is therefore now included in the Mollinedioideae. As its pollen and vegetative and floral anatomy correspond most closely with the other members of this subfamily, I agree with its placement there.

KEY TO THE SPECIES OF *DECARYDENDRON*

- 1a. Leaves abaxially velutinous; petioles 3–5 mm long; tepals of androecious flowers crenulate 1. *D. perrieri*
- 1b. Leaves abaxially glabrate or at most puberulent; petioles 10–20 mm long; tepals of androecious flowers entire, not crenulate.
 - 2a. Laminar teeth 2–4 mm long; androecious flowers with 40–60 stamens 2. *D. helenae*
 - 2b. Laminar teeth 0.5 mm long; androecious flowers with 16–26 stamens 3. *D. lamii*

1. *Decarydendron perrieri* Cavaco, Bull. Soc. Bot. France 105: 38. 1958; Cavaco in Humbert, Fl. Madagascar 80: 9, fig. II:6–8. 1959. TYPE: Madagascar. Tamatave: Analamazaotra forest (near Perinet) (fl), *Perrier de la Bâthie* 10089 (holotype, P).

Monoecious treelet or small tree 5–8 m tall, the base of the trunk swollen, the new growth densely velutinous, the mature leafy stems tomentose. Leaves opposite to subopposite, petiolate; petioles sparsely tomentose, 3–5 mm by 1.5–2 mm; lamina sparsely tomentose adaxially, velutinous abaxially, chartaceous, narrowly elliptic to narrowly ovate, 80–165 mm by 35–65 mm, the apex acuminate, the base broadly cuneate to obtuse, the secondary veins 5–7 pairs, making a 55–65° angle with the costa, depressed adaxially, the venation visible to 3° adaxially, to 4° abaxially, finely reticulate, prominent, the margin serrate-dentate with 30–35 pairs of subequal, acuminate teeth 1–3 mm long. Inflorescence cauliflorous at the swollen base of the trunk, sometimes extending up the trunk for some distance, a velutinous pleiochasium of 5–7 flowers, either unisexual of androecious flowers or sex-

ually mixed and terminated by a gynoeceous flower, the floral axis 120–220 mm by 3–4 mm, the pedicels 5–17 mm by 1.5–3 mm, basally bracteolate. Androecious flowers smaller than the gynoeceous, the receptacle thick, externally velutinous, cupuliform, 7–14 mm diam., the margin bearing 10–18 subequal thick, deltoid-ovate or suborbicular tepals 5–6 mm long by 4–5 mm wide in two series, the external ones crenulate, the internal ones sinuate; stamens ca. 25, glabrous, 2–3 mm long, ellipsoid, the filament short, not prolonged, the anther ovoid, occupying $\frac{2}{3}$ total length of the stamen. Gynoeceous flower at anthesis externally velutinous, cupuliform, thick, 14–17 mm diam., with two longitudinal external ridges, each terminated by an ovate-acuminate, denticulate bracteole, the tepals subequal, deltoid to ovate, 3–6 mm by 5–7 mm, numbering 12–15, in two whorled series, the outer ones externally velutinous, the inner ones glabrate; carpels numerous, ca. 800–1,000, lining the receptacle, free, clavate, ca. 1.5 mm long. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The species is known only from the type locality, where it occurs in *Tambourissa/Weinmannia* wet forest at ca. 900 m.

MADAGASCAR. TAMATAVE: Perinet forest, 900 m, 30 Mar. 1974 (fl), *Cremers* 3017 (MAD).

In addition to the characters cited in the key, *Decarydendron perrieri* differs from its congeners by the presence of a series of smaller tepals alternate with the larger outer series in the female flowers. Further collections, including fruiting material, and field observations are required to further assess its affinities within the genus.

2. *Decarydendron helenae* Danguy, Bull. Mus. Nat. Hist. (Paris), Ser. 1, 34: 279. 1928; Cavaco in Humbert, Fl. Madagascar 80: 10. 1959. TYPE: Madagascar. Fianarantsoa: forest at N base of Ivohibé Peak, 20 Sept. 1926 (fl), *Decary* 5391 (holotype, P).

Small monoecious tree 7 m tall and 25 cm diam., the new growth golden tomentose, the mature leafy stems glabrescent, the trichomes simple or in fascicles of 2. Leaves opposite, petiolate; petioles 10–18 mm by 1.5–2.5 mm, glabrate; lamina ovate-elliptic to narrowly obovate-elliptic, 150–200 mm by 50–130 mm, chartaceous, adaxially hirsutulous when young,

glabrescent, abaxially hirsutulous, velutinous along the costa and veins, the apex acute to shortly and abruptly acuminate, the base narrowly cuneate to obtuse, the secondary veins 5–8 pairs, making a 50–70° angle with the costa, the venation visible to 3° adaxially, to 4° abaxially, the margin prominently serrate-dentate, the teeth 15–25 pairs, unequal, acute to acuminate, 2–4 mm long, the glandular tips indurated. Inflorescence probably cauli- or ramiflorous, a finely velutinous pleiochasium of 5–7 flowers, unisexual of androecious flowers, or sexually mixed and terminated by a gynoecious flower, the floral axis 130–230 mm by 3–4 mm, the pedicels 10–15 mm by 1–1.5 mm, flattened near the junction with the receptacle, basally bracteolate. Androecious flower at anthesis cupuliform to hemispherical, 12–25 mm diam., the margin bearing a single series of 7–15 unequal, obtuse tepals 3–8 mm long by 6–10 mm wide, pilose on both surfaces; stamens ca. 40–60, glabrous, ellipsoid, 3–4.5 mm long, the filament ca. 0.5 mm long, the connective thick, not prolonged, the anther 2.5–4 mm long. Gynoecious flower larger than the androecious, at anthesis the receptacle broadly obconic to cupuliform, 15–35 mm long by 20–40 mm wide, externally pilose-velutinous, the margin bearing a single series of 8–15 thick, obtuse tepals 2–5 mm long by 2–4 mm wide; carpels numerous, up to 300 or more, lining the receptacle, clavate, 1.5–2.5 mm long, glabrous, interspersed with numerous short, simple trichomes. Fruiting receptacle and mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Decarydendron helenae differs from its congeners in having a combination of adaxially glabrate or only sparsely puberulent leaves with large marginal teeth, and more numerous stamens (up to 60 per flower). The species, particularly the variety *stenophyllum*, appears to be most closely allied to *D. perrieri*. More numerous collections and field studies are required to critically assess its status.

KEY TO THE VARIETIES OF
DECARYDENDRON HELENAE

- 1a. Leaves 90–130 mm wide; tepals ca. 15
..... 2a. var. *helenae*
1b. Leaves 50–75 mm wide; tepals 7–10
..... 2b. var. *stenophyllum*

2a. *Decarydendron helenae* var. *helenae*.

Variety *helenae* differs primarily in having larger leaves, a more robust inflorescence, and larger flowers than var. *stenophyllum*. Also, its receptacle lacks the two lateral ridges present in the latter variety. It was named after Helen Decary, who assisted her husband in his botanical research.

Habitat. Known only from the type, which was collected at the base of Ivohibé Peak in the Andringitra Massif in southern central Madagascar, it probably occurs in montane evergreen wet forest, most likely in the upper limits of the *Tambourissa/Weinmannia* zone (Fig. 24).

2b. *Decarydendron helenae* var. *stenophyllum*

Cavaco, Bull. Soc. Bot. France 105: 39. 1958; Cavaco in Humbert, Fl. Madagascar 80: 10. 1959. TYPE: Madagascar. Tulear: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, forest on gneissic laterite, 14–15 Nov. 1928 (fl), *Humbert 6613* (holotype, P; isotypes, K, MAD, US).

In addition to its narrower leaves, variety *stenophyllum* has a less robust inflorescence, smaller flowers with fewer tepals, and floral receptacles with two prominent, lateral ridges ending in small bracteoles. Whether these differences are constant or merely represent stages within a range of variation can only be ascertained by additional collections and field studies. The only known (type) collections of the varieties are, however, geographically separated by about 250 km.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. Variety *stenophyllum* is known only from the southeastern part of Madagascar, probably in the *Tambourissa/Weinmannia* wet forest zone.

- 3. *Decarydendron lamii* Cavaco, Blumea Suppl. 4: 28, fig. 1. 1958; Cavaco in Humbert, Fl. Madagascar 80: 12, fig. II:1–5. 1959. TYPE: Madagascar. Tamatave: Soanierana-Andasibé, 10 Dec. 1938 (fl), *Lam & Meeuse 5835* (holotype, presumably BO, n.v., photo, P; isotype, P).**

Small monoecious understory tree 5 m tall, the new growth fulvous-velutinous, the mature

leafy stems villous, 3–5 mm diam. Leaves opposite, petiolate; petioles 10–20 mm by 1.5–2 mm, velutinous; lamina chartaceous, narrowly elliptic to narrowly obovate-elliptic, 100–190 mm by 40–72 mm, the apex abruptly short acuminate, the base cuneate, the adaxial surface glabrate, the abaxial surface appressed pilose, especially on the costa and veins, the secondary veins 10–12 pairs, making a 65–75° angle with the costa, raised on both surfaces, the venation visible to 3° adaxially and to 4° abaxially, the margin plane, finely dentate, the teeth 40–50 pairs, 0.5 mm long, glandular tipped. Inflorescence cauliflorous from meristematic swellings on the trunk or ramiflorous, a pleiochasium of 8–15 flowers, unisexual of androecious flowers or sexually mixed and terminated by a single gynoeceous flower, the floral axis 100–220 mm by 2 mm, densely fulvous-velutinous. Androecious flowers smaller than the gynoeceous, at anthesis shallowly cupuliform to disciform, open, 12–16 mm diam. by 5–8 mm long, externally finely strigose-sericeous, the margin bearing 10–12 entire, obtuse, ovate to ligulate tepals 2–3 mm wide and long, in two series, the pedicel 6–25 mm by 1 mm, basally bracteolate, the bracteole to 4 mm long; stamens 16–26, ellipsoid to obovoid, 1.8–3 mm long by 1.5–1.8 mm wide, the filament distinct, short, the anther occupying $\frac{2}{3}$ – $\frac{3}{4}$ total length of the stamen, the connective thick, not prolonged, the internal receptacle surface glabrous, purple. Gynoeceous flower at anthesis obconical, 30 mm diam. by 24 mm long, externally finely velutinous, the carpels numerous (probably ca. 500 or more), lining the receptacle. Fruiting receptacle and mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The species is known from the lower montane wet forest zone of Myristicaceae/*Anthostema* in the eastern region, below 900 m.

MADAGASCAR. DIEGO SUAREZ: S slope of Betsomanga, Bassin of Androranga River, 700 m, 18 Nov. 1950 (fl), *Capuron 827-SF* (P). TAMATAVE: Andapa District, eastern slopes of the Marojejy Massif, Lokoho River basin, E of Ambalamansy II, 450–800 m, rain forest on gneissic laterite, 28 Nov. 1948 (st), *Humbert & Capuron 22154* (MO).

In addition to the characters cited in the key, *Decarydendron lamii* differs from its congeners in that the androecious flowers are purple within. Like the other species in the genus, it is poorly known.

Ehippiandra Decne., Ann. Sci. Nat. (Paris), Ser. 4, 9: 278, pl. 7. 1858; A.DC., Prodr. 16(2): 662. 1868; Baill., Hist. Pl. ed. 1, 1: 304. 1869; Perk., Engl. Bot. Jahrb. 25(4–5): 551, t. 5: 1–5. 1898; Perk. & Gilg, Pflanzenr. 4, 101: 50, fig. 9. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 15. 1911; Perk., Gatt. Monim. 32, fig. 19. 1925; Cavaco, Bull. Soc. Bot. France 104: 610. 1957; Cavaco in Humbert, Fl. Madagascar 80: 4. 1959; Hutch., Gen. Fl. Pl. 1: 117. 1964. TYPE: *E. myrtoidea* Decne.

Hedycaryopsis Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 278. 1928, synonym. nov. TYPE: *H. madagascariensis* Danguy.

Monoecious shrubs, treelets or trees 10–25 m tall, the trunk attaining 50 cm diam., the new growth pubescent to glabrate, the hairs simple. Leaves opposite to subopposite, petiolate, subglabrous or $\pm$ pubescent abaxially, especially along the costa and veins, the venation festooned brochidodromous, semicraspedodromous or craspedodromous, the margin entire or sparsely dentate apically with acute, glandular teeth, or sinuate-dentate with rounded, apically depressed glandular teeth; juvenile and sucker leaves unknown. Inflorescence axillary, terminal, or ramiflorous on leafless stems, a short, 5-flowered unisexual pleiochasium or a 3–5-flowered sexually mixed dichasium, the gynoeceous flower solitary and terminal, maturing first, the androecious flowers lateral, or the flowers solitary and axillary, the pedicels $\pm$ long and slender, basally bracteolate. Androecious flower in bud globose to ellipsoid, bearing 2–4(–5) small tepals apically, at anthesis splitting deeply into 4(–5) $\pm$ regular valvate segments, these spreading flat or reflexing, the apex often bearing 1–2 obtuse, scale-like tepals internally; stamens eglandular, ca. 9–50, situated irregularly or in several series on the glabrous to puberulent internal receptacle surface, ligulate to shortly deltoid, the filament broad, short or sessile, the anther tetrasporangiate, the 2 loculi lateral and separate or connivent or confluent apically, longitudinally dehiscent, extrorse; pollen inaperturate, spheroid to ovoid, the exine thick, the sexine granulate with few to many, small to large scattered verrucae or gemmae. Gynoeceous flower in bud subglobose-discoid, concave, the margin usually bearing 4–8(–16) small, decussate deltoid tepals; at anthesis expanding gradually, not splitting, broadly obconic to discoid, the torus flat to concave, bearing ca.

15–120 free, short sessile, 4–6-sided columnar carpels ca. 1–1.5 mm long, the apex flat, the small stylar canal lateral, medial, the ovary unilocular, the solitary ovule anatropous, situated in a small locule near the base of the carpel, the carpels interspersed with short, simple hairs. Fruiting receptacle discoid, enlarged, fleshy and red when fresh, the flat to convex surface bearing ca. 10–75 free carpels, each surrounded basally by a cupule for $\frac{1}{3}$ – $\frac{1}{2}$ its length; mature carpels ovoid to ellipsoid, 7–12 mm long, the thin fleshy mesocarp ripening black, the endocarp thin, horny, pale brown, the surface scrobiculate, the endosperm fleshy. Chromosome number unknown.

Distribution. All six species are endemic to Madagascar (Figs. 25, 26).

Habitat. The genus ranges from lower montane wet and cloud forest to high altitude montane sclerophyllous forest and ericoid formations.

TAXONOMIC HISTORY OF *EPHIPPIANDRA*

The genus *Ephippiandra*, described by Decaisne in 1858 based on *E. myrtoidea*, was named in reference to the low, saddle-shaped anthers characteristic of the species. A second species, described by Perkins (1911) as *Tambourissa microphylla*, was subsequently transferred to *Ephippiandra* by Cavaco (1957a). In the same year Cavaco (1957c) described a third species and established two sections in the genus based on the presence (section *Staminodia*) or absence (section *Ephippiandra*) of fleshy tepals on the inner tips of the receptacle lobes, which he referred to as “staminodes.”

Danguy described *Hedycaryopsis* in 1928 based on *H. madagascariensis*, and Cavaco (1958c) subsequently described three additional species preceding his treatment for “Flore de Madagascar” (1959).

GENERIC DELIMITATIONS AND SYSTEMATIC POSITION OF *EPHIPPIANDRA*

Danguy (1928) established *Hedycaryopsis* as a segregate genus primarily on the basis of its gynoeceous flowers, which he felt approached those of *Hedycarya* Forst. (syn. *Carnegieodoxa* Perk.) from Oceania. The discoid to broadly obconic gynoeceous flowers of *Hedycaryopsis*, like those of *Ephippiandra*, are usually bordered by several pairs of minute, decussate deltoid tepals and the torus bears few to numerous free, sessile poly-

hedral-columnar carpels on its surface (15–38 in *Ephippiandra*; 22–120 in *Hedycaryopsis*; Fig. 14F, G). Furthermore, carpels of both possess oblique lateral stylar canals (Fig. 13C, D). Danguy apparently never examined gynoeceous flowering material of *Ephippiandra*, because he makes no mention of it in his discussion (the type of *E. myrtoidea* has only androeceous flowers and fruit). Clearly, gynoeceous floral morphology does not support segregation of *Hedycaryopsis* from *Ephippiandra*.

Furthermore, fruiting receptacles of both genera are morphologically identical. Mature fruiting receptacles in both consist of a fleshy, discoid torus, red when ripe, bearing few to many ovoid to ellipsoid carpels surrounded basally by cupules (Fig. 14H). Carpels of both have a thin mesocarp, green when fresh, overlying the thin, horny endocarp. Understandably, fruiting characters have never been used to distinguish the genera.

Although Danguy (1928) noted that androeceous flowers of *Hedycaryopsis* scarcely differed from those of *Tambourissa*, Cavaco (1957c, 1959) felt that stamens were a stable key character separating *Ephippiandra* from *Hedycaryopsis* and *Tambourissa*. He stated that in *Ephippiandra* the stamens were sessile and broader than long (“déprimées”) with the loculi apically confluent into a single, crescentiform loculus, as opposed to *Hedycaryopsis* which had separate, lateral loculi and an apically prolonged connective. He ignored, or at least failed to mention, however, that in species such as *E. myrtoidea* the loculi may be both connivent as well as confluent in the same flower. *Tambourissa* displays the entire range of conditions and the loculi may be separate, connivent, or confluent not only apically but basally as well in various species. Two or more of these conditions may occur in a single androeceous flower of *T. cordifolia* (Fig. 42C–E). Other species such as *T. purpurea* possess broad, sessile stamens with a single loculus similar to those of some *Ephippiandra* species. Furthermore, the number of stamens is relatively small in both and overlaps (10–36 in *Ephippiandra*; 9–26 in *Hedycaryopsis*), as does the presence or absence of tepals on the extremities of the receptacle lobes. Androeceous floral morphological characters are therefore clearly insufficient for generic segregation.

Examination of the pollen of two species each of *Ephippiandra* and *Hedycaryopsis* (Lorence, 1980; Lorence et al., 1984) has revealed that their

sexinous patterns correspond much more closely to each other than to any of the other Malagasy genera. Pollen of *E. microphylla* and *E. myrtoidea* both have thick, granulate to verrucate sexines with larger, scattered gemmae and folds occurring in the latter. In *H. perrieri* and *H. tsaratanensis* the sexine is also thick and granulate with large, dome-shaped verrucae and gemmae. Sexinous patterns in these two genera differ primarily in the size of the processes, but correspond much more closely to each other than to the remaining Malagasy genera. I do not feel that pollen supports separation of the two genera.

Cavaco (1959) further distinguished these genera on the basis of inflorescence structure: dichasial with a central gynoeceous flower and lateral (rarely solitary) androeceous flowers in *Hedycaryopsis* (Fig. 14F, G); solitary or pleiochasial in *Ehippiandra*. The only species supposedly having pleiochasia, *Ehippiandra capuronii*, actually belongs in *Tambourissa* (see below). Collections of *E. myrtoidea* (Anon. sub Herb. ORSTOM 3366, MAD; Anon. sub Herb. Alaotra 300, MAD) possess sexually mixed dichasia, however, thus undermining the validity of this character in separating the genera. Furthermore, an even greater range of inflorescence types occurs in the otherwise very cohesive genus *Tambourissa*.

Leaves of the various *Hedycaryopsis* species are extremely diverse and display a striking array of venation patterns (see section on Leaf Architecture). For example, leaves of the type species, *H. madagascariensis*, are highly specialized and generally characterized by open craspedodromous venation ending in sunken teeth at the sinuate-dentate margin (Fig. 6F), a pattern apparently derived from the brochidodromous condition (R. Keating, pers. comm.). In this respect, they differ strikingly from all other known Monimiaceae genera and may have influenced Danguy (1928) to describe the genus as new. Venation in two other species, *H. capuronii* (= *Ehippiandra domatiata*; Fig. 6C, D) and *H. tsaratanensis* (Fig. 6E), as well as some collections of *H. madagascariensis*, is transitional between craspedodromous and brochidodromous, thus linking it to *H. perrieri* (Fig. 6B) which has festooned brochidodromous venation typical of virtually all other genera of Monimiaceae, including *Ehippiandra myrtoidea* (Fig. 6A) and *E. microphylla*. This intergrading range of venation patterns provides another criterion for uniting the two genera.

Because there seems to be no basis for continued segregation of *Hedycaryopsis*, I propose that it be reduced to synonymy under *Ehippiandra*, which would thus encompass six species, necessitating one new name and three new combinations given below.

Among the Malagasy Monimiaceae belonging to the Mollinedioideae, *Ehippiandra* occupies a position intermediate between *Decarydendron* and *Tambourissa* in terms of floral morphological specialization. The strong androeceous/gynoeceous floral dimorphism, highly reduced tepals, sessile carpels enveloped basally by cupules in fruit, androeceous receptacle closed in bud and splitting open at anthesis, and tendency towards short, sessile stamens with confluent loculi are all specializations over *Decarydendron*. Female floral construction in *Ehippiandra* is not so advanced as in *Tambourissa*, however, where the closed gynoeceous receptacle splits partly open at anthesis and the carpels are inferior and syncarpous.

KEY TO THE SPECIES OF *EPHIPPIANDRA*

- 1a. Leaf margin sinuate-dentate with rounded, apically $\pm$ depressed teeth.
 - 2a. Abaxial laminar surface densely ferruginous tomentose; floral pedicel 25–50 mm long, ferruginous tomentose 1. *E. tsaratanensis*
 - 2b. Abaxial laminar surface at most grayish or yellowish puberulent along costa and veins; floral pedicel 8–15 mm long, grayish canescent or villous 2. *E. madagascariensis*
- 1b. Leaf margin entire or at most with 1–2 pairs of acute, deltoid teeth in apical portion.
 - 3a. Basal pair of secondary veins extending up to or beyond middle portion of lamina before joining next pair above; barbate domatia present abaxially in secondary vein axils 3. *E. domatiata*
 - 3b. Basal pair of secondary veins joining next pair above before attaining middle of lamina; domatia absent abaxially in secondary vein axils.
 - 4a. Apex of lamina retuse, folded downward into a thickened flap 4. *E. perrieri*
 - 4b. Apex of lamina shortly acuminate to acute or rounded, not retuse or thickened into a flap.
 - 5a. Inner portion of each androeceous floral receptacle lobe bearing 1(–2) scale-like tepals 6. *E. microphylla*
 - 5b. Inner portion of androeceous floral receptacle lobes lacking scale-like tepals 5. *E. myrtoidea*

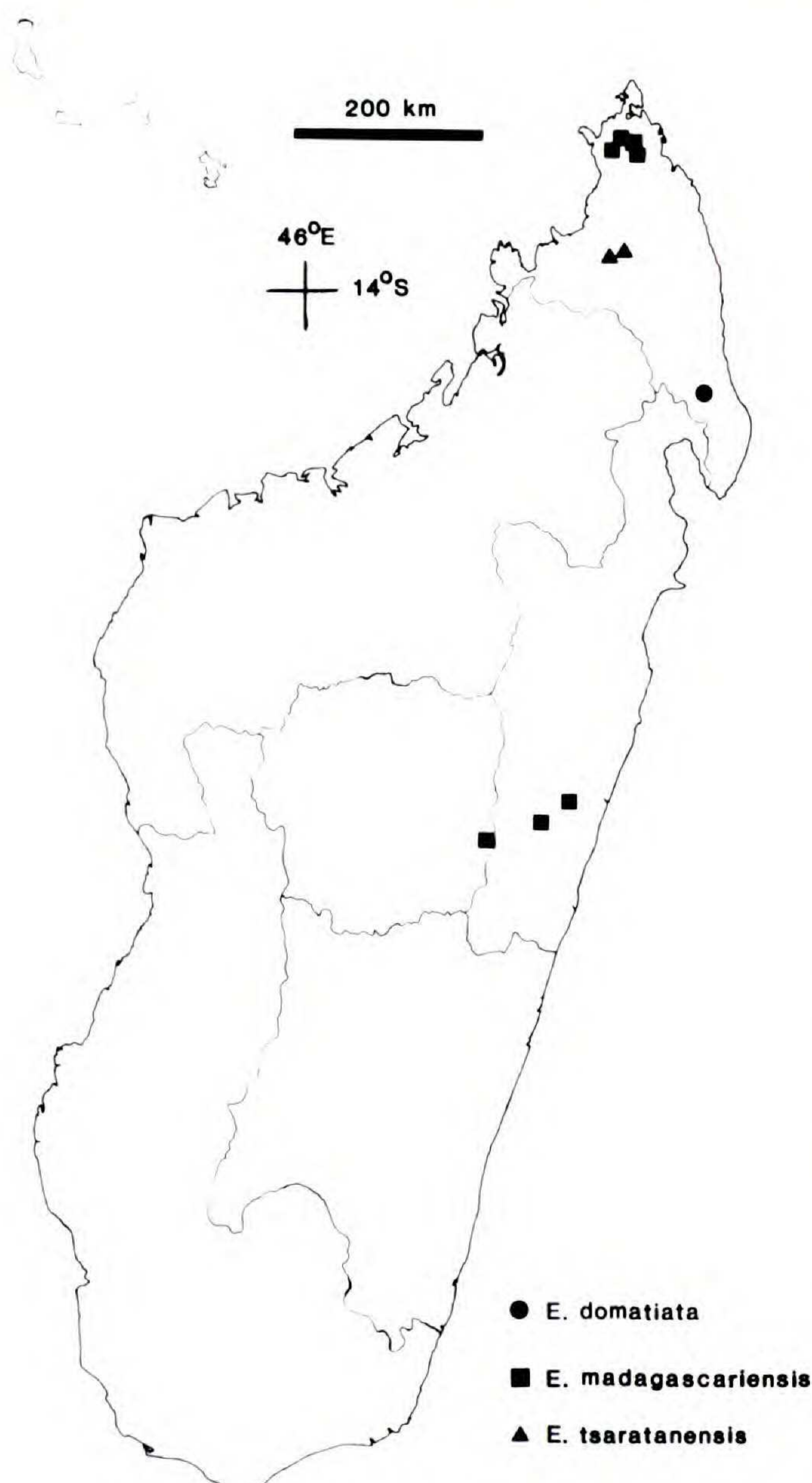


FIGURE 25. Distribution map of some *Ehippiandra* species in Madagascar.

1. ***Ehippiandra tsaratanensis*** (Cavaco) Lorence, comb. nov. *Hedycaryopsis tsaratanensis* Cavaco, Bull. Soc. Bot. France 105: 41. 1958; Cavaco in Humbert, Fl. Madagascar 80: 14, fig. III:1–5. 1959. TYPE: Madagascar. Diego Suarez: Tsaratanana Massif, forest with herbaceous undergrowth, 1,800 m (fl), *Perrier de la Bâthie* 15302 (holotype, P).

Monecious tree 10–25 m tall, the new growth densely ferrugineous tomentose, the mature leafy stems sparsely tomentose. Leaves opposite to subopposite, petiolate; petioles 8–15 mm by 2.5–3.5 mm, ferrugineous tomentose; lamina subcoriaceous, the apex rounded, obtuse, the tip depressed, the base broadly cuneate, rounded, truncate or rarely subcordate, adaxially pubescent, glabrescent, abaxially densely ferrugineous to-

mentose, the secondary veins 5–8 pairs, making a 50–65° angle with the costa, the venation craspedodromous or partly brochidodromous, visible to 3° adaxially, to 4° abaxially, the margin slightly revolute, sinuate with 5–8 pairs of broadly rounded, apically depressed teeth. Inflorescence axillary, ferrugineous velutinous, a 3–5-flowered, sexually mixed dichasium, the 2–4 androecious flowers lateral, the gynoecious flower terminal and maturing first, the peduncle 15–30 mm by 2–3 mm, apically dilated, the pedicels each subtended by a linear bracteole 4–6 mm long. Androecious flower in bud ellipsoid to globose, 4–6 mm diam., ferrugineous tomentose, bearing near the apex 4 linear-ovate tepals 3–4 mm long, the pedicel 25–50 mm by 1 mm; at anthesis deeply 4-fid, 12–15 mm diam., the lobes spreading flat, each bearing a broad tepal apically within; stamens 18–20, ovate to ligulate, 2–2.5 mm long by 1–1.5 mm wide, slightly incurved, the filament thick, short or sessile, the loculi lateral, separate, occupying almost entire length of the stamen, the connective slightly prolonged, apiculate. Gynoecious flower at anthesis broadly obconical, concave, externally ferrugineous tomentose, 14–18 mm wide by 7–8 mm long, the margin bearing several minute, deltoid tepals, the pedicel 32–37 mm long; carpels 40–70, lining the receptacle, columnar, 4–5-sided, 1–1.5 mm long. Mature fruiting receptacle red when fresh, drying dark brown, irregularly discoid, convex, 60–85 mm diam., the ground tissue containing numerous stone cells, bearing (4–)40–70 free carpels surrounded basally by cupules for $\frac{1}{3}$ – $\frac{1}{2}$ their length, the pedicel and peduncle ca. 45 mm long by 3–4 mm diam.; mature carpels ovoid-ellipsoid, 10–12 mm long by 6–7 mm diam., green when fresh, drying brown, the mesocarp thin, fleshy, the endocarp whitish, 0.2 mm thick, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. The species is known only from the type locality on the Tsaratanana massif in north central Madagascar where it occurs from ca. 1,800 to 2,500 m, presumably in montane sclerophyllous cloud forest.

MADAGASCAR. DIEGO SUAREZ: Tsaratanana massif, trail up S ridge of Maromokotro, Andohanisambirano, 2,000–2,500 m; montane cloud forest, 9 May 1974 (fl, fr), *Gentry* 11605 (MO).

The species is most closely allied to *Ehippiandra madagascariensis*, from which it differs

by its suborbicular, abaxially ferrugineous tomentose leaves with mixed craspedodromous/brochidodromous venation, its more densely ferrugineous tomentose parts, more robust inflorescence with longer pedicels subtended by long, linear bracteoles, and by its androecious buds bearing 4 long, linear-ovate tepals.

2. *Ehippiandra madagascariensis* (Danguy)

Lorence, comb. nov. *Hedycaryopsis madagascariensis* Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 278. 1928; Cavaco in Humbert, Fl. Madagascar 80: 14, fig. IV:1–6. 1959. TYPE: Madagascar. Diego Suarez: Antsalaky forest, 700–1,000 m, 17 Oct. 1927 (fl, fr), *Ursch* 66 (lectotype, P, here designated).

Monoecious tree 10–25 m tall and 50 cm diam., the new growth grayish to yellowish pubescent or canescent, the mature leafy stems 3–5 mm diam., puberulent. Leaves opposite to subopposite, petiolate; petioles puberulent, 8–15 mm by 1.5 mm; lamina subcoriaceous, $\pm$ bullate, obovate-elliptic to suborbicular, 30–90 mm by 22–60 mm, the apex obtuse, rounded, the tip retuse, the base cuneate, the adaxial surface sparsely puberulent, glabrescent, the abaxial surface puberulent, especially along the costa and veins, the secondary veins 3–5 pairs, making a 40–50° angle with the costa, depressed adaxially, prominent abaxially, dichotomizing and running into the marginal teeth, the venation craspedodromous, rarely semicraspedodromous, visible to 2° adaxially, to 3° abaxially, the margin revolute, sinuate with 2–7 pairs of broadly obtuse, apically depressed teeth. Inflorescence axillary, a sexually mixed, 3–5-flowered dichasium, the 2–4 androecious flowers lateral, subtending the terminal gynoecious flower, or the gynoecious flower rarely solitary, the peduncle grayish pubescent, 15–30 mm by 1–1.5 mm, apically dilated. Androecious flower in bud globose, 3–4 mm diam., the canescent pedicel 8–20 mm by 0.6–0.8 mm, each subtended by a naviculate bracteole 2 mm long, the apex bearing 3–4 obtuse, puberulent tepals 1–2 mm long; at anthesis deeply 4(–5)-fid, ca. 10 mm diam., the lobes spreading flat; stamens 35–50, ligulate-subulate, 1.5–2 mm long by 0.7 mm wide, the filament thick, subsessile, the loculi lateral, separate, occupying almost entire length of the stamen, the connective thick, prolonged, obtuse, the internal receptacle surface glabrous. Gynoecious flower at anthesis discoid,

flat, 10–15 mm diam. by 1.5 mm thick, externally canescent, the margin bearing 8 or 16 minute, deltoid tepals 0.5 mm long, the pedicel canescent, 6–15 mm by 1.5 mm; carpels ca. 140–150, lining the receptacle, sessile, columnar, 5–6-sided, 0.8–1 mm long by 0.6–0.8 mm wide, the apex flat, interspersed with numerous short, simple hairs, the internal receptacle surface with mucilaginous secretion. Mature fruiting receptacle swollen, everted, 35–60 mm diam., bearing 30–50 carpels, the pedicel and peduncle ca. 25 mm by 3 mm; carpels ovoid-ellipsoid, 8–10 mm long by 6–7 mm diam., the basal $\frac{1}{4}$ – $\frac{1}{3}$ enveloped by a cupule, the mesocarp reddish, fleshy, ca. 0.5 mm thick, the endocarp brown, foveolate-reticulate.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. *Ehippiandra madagascariensis* appears to be primarily restricted to the *Tambourissa/Weinmannia* wet forest zone (ca. 700–1,000 m) in northern and eastern Madagascar.

MADAGASCAR. DIEGO SUAREZ: Montagne d'Ambre, S of Les Roussettes Forestry Station by Petit Lac and above on the summit, 1,100–1,200 m, 22 Dec. 1967 (fl), *Bernardi* 11977 (K, MO); Montagne d'Ambre National Park, mature wet forest, ca. 1,200 m, 23 May 1974 (fr), *Gentry* 11962 (MO); Montagne d'Ambre, Dec. 1964 (st), *Morat* 1182 (MAD, P); 1,100 m, 7 Dec. 1952 (st), *Schedl* 170 (MAD); (st), *Schedl* 177 (MAD). TAMATAVE: Beandy, Perinet, 12 Sept. 1948 (fl), *Anon. sub Service Forestier* 1596-SF (MAD); Analamazaotra forest (Perinet), 1919 (fr), *Thouvenot* s.n. (P, syntype of *Hedycaryopsis madagascariensis*); road from Anosibé to Moramanga, 9 May 1969 (st), *Anon. sub Service Forestier* 26852-SF (MO, P). TANANARIVE: Ahimadana Canton, Andramasina, forest SE of Lake Tsiazompaniry, May 1961 (fl), *Capuron* 20278-SF (MO).

The species is most closely allied to *Ehippiandra tsaratanensis*, differing by its obovate, abaxially glabrous or sparsely puberulent leaves with open dichotomous, craspedodromous (rarely partly brochidodromous) venation, its yellowish to grayish canescent pubescence, and less robust inflorescence with shorter pedicels, bracteoles, and androecious tepals. It yields a yellowish wood said to be good for construction.

Vernacular names. Ambora, Amborabé, Tambonaika (Madagascar).

3. *Ehippiandra domatiata* Lorence, nom. nov.

Hedycaryopsis capuronii Cavaco, Bull. Soc. Bot. France 105: 40. 1958; Cavaco in Hum-

bert, Fl. Madagascar 80: 13. 1959 non *Ehippiandra capuronii* Cavaco, Bull. Soc. Bot. France 104: 610. 1957. TYPE: Madagascar. Diego Suarez: Beanjada Massif (N of the Masoala Peninsula), ridge at ca. 1,100 m, 30 Dec. 1953 (fl), *Capuron 8828-SF* (holotype, P).

Monoecious shrub, the new growth with sparse, scattered hairs, glabrescent, the mature leafy stems 1–2 mm diam., becoming lenticellate. Leaves opposite, petiolate; petioles glabrous, 6–10 mm by 0.7–1 mm; lamina glabrous, chartaceous, obovate-elliptic to rhombic, 25–40 mm by 14–25 mm, the apex obtuse to retuse, often apiculate, the base cuneate, the secondary veins 2–3 pairs, the strong basal pair making a 40–45° angle with the costa, attaining top half of the lamina before uniting brochidodromously with the next pair, adaxially depressed, abaxially prominent, the axils of the basal veins domatiate and barbate abaxially, the venation visible to 2° adaxially and to 3–4° abaxially, the margin revolute, with 1–2(–3) pairs of minute teeth in the apical $\frac{1}{2}$ – $\frac{1}{3}$. Inflorescence axillary, a 3-flowered dichasium, the terminal gynoecious flower subtended by 2 androecious flowers, or the male flowers solitary or in cymes of 3, the peduncle glabrous, (4–)12–15 mm by 0.5 mm, with 2 basal bracteoles. Androecious flower in bud globose, 2.5–3 mm diam., glabrous, the apex with 2 pairs of broadly obtuse tepals 1.5–2 mm wide, the pedicel 7–8 mm by 0.5 mm, subtended by a bracteole 1–1.5 mm long; at anthesis deeply 4-fid, 5–6 mm diam., the lobes spreading flat, each bearing apically 2 thin, broadly obtuse tepals internally; stamens 9–10, ovoid-subulate, 1–1.5 mm long by 0.6–0.8 mm wide, the filament short, distinct, the loculi lateral, separate, occupying ca. $\frac{3}{4}$ total length of the stamen, the connective slightly prolonged, apiculate. Gynoecious flower at anthesis discoid, flat, 4.5–5 mm diam. by 1.5 mm thick, externally with a few scattered hairs, the margin entire or with a few minute, deltoid teeth, the pedicel glabrous, 9–19 mm by 0.5 mm, occasionally basally bracteolate; carpels 24–25, sessile, columnar, 0.8 mm long by 0.6–0.7 mm wide, 5–6-angled, interspersed with tufts of short, simple hairs. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 25).

Habitat. The species is known only from the type locality, presumably in *Tambourissa/Weinmannia* wet forest at ca. 1,100 m.

Ehippiandra domatiata is readily distinguishable from its congeners by its glabrous inflorescence and stems, and particularly by its leaves with abaxially domatiate, barbate secondary vein axils. Further collections, especially fruiting material, and field observations are greatly desired.

4. *Ehippiandra perrieri* (Cavaco) Lorence, comb. nov. *Hedycaryopsis perrieri* Cavaco, Bull. Soc. Bot. France 105: 40. 1958; Cavaco in Humbert, Fl. Madagascar 80: 16. 1959. TYPE: Madagascar. Diego Suarez: Tsaratanana massif, forest with herbaceous understory, 2,000 m, Apr. 1929 (fl, fr), *Perrier de la Bâthie 16249* (holotype, P).

Monoecious shrub, treelet or tree 12–15 m tall, the new growth finely cinereous pubescent, the mature leafy stems 2–3 mm diam., grayish puberulent, glabrescent, often with large, elliptic lenticels. Leaves opposite to subopposite, petiolate; petioles 5–11 mm by 1 mm, finely puberulent, glabrescent; lamina chartaceous to subcoriaceous, glabrous, elliptic to obovate or obcordate, 25–55 mm by 15–35 mm, the apex obtuse, rounded, the tip retuse or emarginate, folded under into a thickened flap, the base narrowly cuneate, the secondary veins 3–4 pairs, making a 45–55° angle with the costa, obscure adaxially, prominent abaxially, the venation visible to 3° adaxially and to 4° abaxially, the margin entire, $\pm$ revolute. Inflorescence axillary, a 3-flowered, sexually mixed dichasium, the gynoecious flower terminal, subtended by a pair of androecious flowers, or the androecious flowers solitary, axillary, the peduncle 10–15 mm by 1 mm, finely puberulent, subtended by several small, deltoid bracteoles. Androecious flower in bud globose, 3 mm diam., with scattered appressed hairs, the apex bearing 2 obtuse to subulate, ciliate tepals 1–1.5 mm long, the pedicel 8–20 mm by 0.7 mm, often with 1–2 minute bracteoles; at anthesis deeply 4–5-fid, 9–10 mm diam., the lobes spreading flat or recurving slightly, internally glabrous, each terminated by a broad, retuse or bifid tepal internally; stamens 15–20, recurved, 2–2.5 mm long, the filament slender, 1–1.5 mm long, the anther ovoid-ellipsoid, 1 mm long, the loculi lateral, separate, the connective prolonged, apiculate. Gynoecious flower on a pedicel 12–20 mm by 1 mm, bracteolate basally or medially, the receptacle open in bud; at anthesis flat, discoid, 4–6 mm diam. by 2 mm thick,

externally finely gray sericeous, the margin bearing 4–8(–16) minute, deltoid tepals ca. 0.5 mm long; carpels 20–25, bluntly columnar, 1 mm long by 0.6–0.8 mm wide, 5–6-angled, covering the torus, interspersed with short, simple hairs. Mature fruiting receptacle swollen, 15–20 mm diam., usually with 2–4 carpels, the pedicel and peduncle 25–45 mm by 1.5 mm; carpels ovoid, 8–9 mm by 6–7 mm, the basal $\frac{1}{4}$ – $\frac{1}{3}$ enclosed by a raised cupule, the mesocarp thin, fleshy, the endocarp light brown, striate-reticulate.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species is restricted to sclerophyllous montane cloud forest and ericoid formations on Madagascar's highest mountains, the Marojezy and Tsaratanana massifs, from ca. 2,000 to 2,650 m.

MADAGASCAR. DIEGO SUAREZ: Marojezy (Marojezy) massif, summit, 29 Mar. 1949 (fl, fr), *Anon. sub Herb Alaotra* 3479 (MAD, 3 sheets); Marojezy Natural Reserve, sclerophyllous forest, 2,000 m, 27 Nov. 1972 (fl), *Guillaumet* 4058 (MAD); ericoid scrub on the summit of Marojezy, 2,000–2,137 m, Dec. 1972 (fl), *Morat* 4035 (MAD, P); Tsaratanana massif, 2,200–2,650 m, Nov. 1966 (fl), *Capuron* 25000-SF (MO, P); 2,100 m, Nov. 1966 (fr), *Morat* 2268 (MAD, P); Andohanisambirano, 2,500 m, Nov. 1966 (fl), *Morat* 2332 (MAD); (fr), *Morat* 2333 (MAD).

Ehippiandra perrieri most closely resembles *E. domatiata*, but its leaves have entire margins, a more deeply retuse or emarginate apex which is thickened and folded under into a flap, lack domatia, and the inflorescence is sparsely pubescent. In sheltered forest *E. perrieri* becomes a tree, but takes on a shrubby habit on exposed slopes.

5. ***Ehippiandra myrtoidea*** Decne., Ann. Sci. Nat. (Paris), Ser. 4, 9: 278, pl. 7. 1858; A.DC., Prodr. 16(2): 662. 1868; Baill., Hist. Pl. ed. 1, 1: 304. 1869; Perk., Engl. Bot. Jahrb. 25(4–5): 551, t. 5:1–5. 1898; Perk. & Gilg, Pflanzenr. 4, 101: 51, fig. 9. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 15. 1911; Perk., Gatt. Monim. 32, fig. 19. 1925; Cavaco in Humbert, Fl. Madagascar 80: 6, fig. I:7–9. 1959. *Mollinedia myrtoidea* (Decne.) Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902. TYPE: Madagascar. Tananarive: vicinity of Tananarive (fl), *Goudot s.n. in 1840* (holotype, P).

Monoecious treelet 3–4 m tall, densely branch-

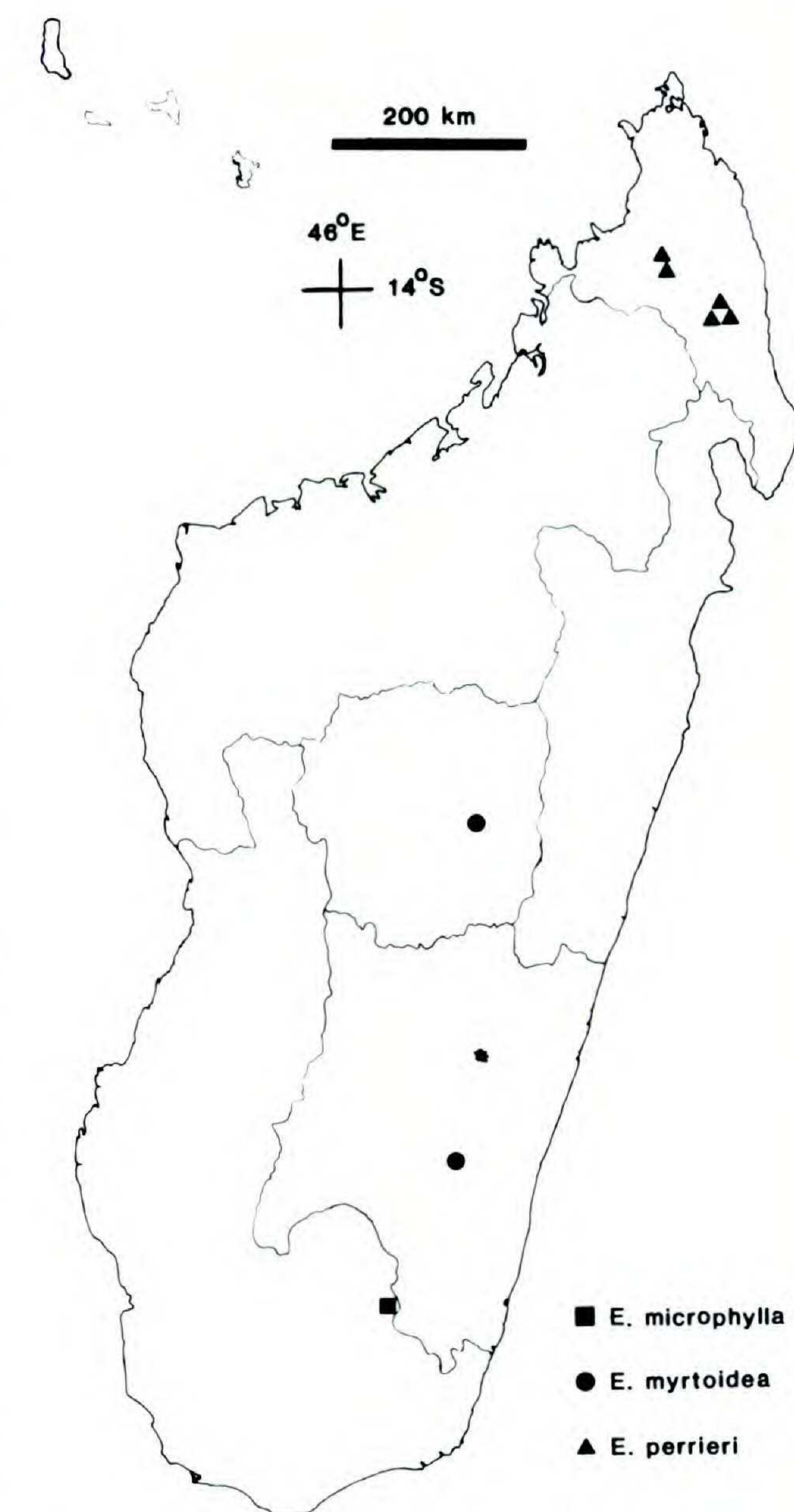


FIGURE 26. Distribution map of some *Ehippiandra* species in Madagascar.

ing, the new growth sparsely appressed pilose, the mature leafy stems 1.5–2 mm diam., shortly velutinous-tomentose, the hairs pale yellowish brown. Leaves opposite, shortly petiolate; petioles 1–5 mm by 1 mm, velutinous-tomentose; lamina chartaceous to subcoriaceous, ovate to elliptic, 12–30 mm by 8–22 mm, the apex acute to abruptly short acuminate, the tip thickened, the base cuneate to obtuse or rounded, adaxially with a few appressed hairs when young, abaxially with hairs along the costa and margin, the secondary veins 3–6 pairs, making a 65–85° angle with the costa, the venation obscure adaxially, visible to 2° abaxially, the margin entire, pilose, slightly revolute. Inflorescence axillary or terminal, a 3–5-flowered dichasium with a single terminal gynoeceous flower subtended by 2–4 androeceous flowers, or the flowers axillary, solitary

or in cymes of 2–3, the peduncle 3–4 mm by 1 mm, pubescent, basally bracteolate. Androecious flower in bud globose, 2–4 mm diam., with scattered hairs, the apex apiculate with 1–2 pairs of small, obtuse tepals to 1 mm wide, the pedicel 2.5–20 mm by 0.6 mm, bracteolate; at anthesis deeply 4-fid, 6–8 mm diam., the lobes spreading flat, each usually terminated by a small, obtuse tepal externally; stamens 10–13, 2–3 per lobe, sessile, obtuse, 1 mm long by 1.5–2.5 mm wide, the loculi connivent or usually confluent apically into a single crescentiform loculus, the filament broad, short or sessile, the inner receptacle surface glabrous. Gynoecious flower on a pedicel 6–25 mm by 0.8 mm; at anthesis the receptacle discoid, flat or $\pm$ concave, 6–8 mm diam. by 1 mm thick, the surface crowded with 25–30 sessile, 4–6-sided columnar carpels 0.8–1 mm long by 0.7–0.9 mm wide, interspersed with short, simple hairs. Mature fruiting receptacle terminal, the torus swollen, convex, 15–30 mm diam., red when fresh, drying black, the surface sparsely pubescent, bearing (1–)3–14 carpels, the pedicel and peduncle 25–50 mm by 1.5–2.5 mm; carpels ovoid to ellipsoid, 8–9 mm by 5–6 mm, the basal $\frac{1}{3}$ – $\frac{1}{2}$ surrounded by a raised cupule, the mesocarp black when ripe, drying blackish, thin, fleshy, the endocarp thin, brown, the surface finely scrobiculate.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species appears to be restricted to the *Tambourissa/Weinmannia* montane sclerophyllous forest and high altitude ericoid zones of eastern and central Madagascar, from ca. 1,300 to 2,000 m.

MADAGASCAR. FIANARANTSOA: high valley of the Rienana (Basin of the Matitanana River), forest, 1,000–1,400 m, 18–22 Nov. 1924 (fl), *Humbert 3447* (K). PROVINCE UNCERTAIN: Manijarivolo-Andrianony, 1,650 m, 30 Oct. 1970 (fl), *Anon. sub Herb. ORSTOM 3366* (MAD); Central Madagascar (fl), *Baron 1263* (K); (fr), *Baron 1355* (K); Andrangaloatra (fr), *Parker s.n. in 1881* (K); Andohakelo Massif (R.N. 11), 1,800–1,850 m, Jan. 1974 (fl, fr), *Morat 4430* (P); *Morat 4434* (P); *Morat 4480* (P). WITHOUT PRECISE LOCALITY: (fl), *Anon. sub Herb. Alaotra 300* (MAD).

The species is virtually indistinguishable from *Ehippiandra microphylla* except for its androecious flowers which have fewer stamens and lack tepals on the inner apical portion of the receptacle lobes. Pedicel length and inflorescence type intergrade, and further collections and field studies are necessary to ascertain whether the taxa

are distinct or merely represent variations of a single, polymorphic species.

6. *Ehippiandra microphylla* (Perk.) Cavaco, Kew Bull. 12: 228. 1957; Cavaco in Humbert, Fl. Madagascar 80: 7, fig. III:6–9. 1959. *Tambourissa microphylla* Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911. TYPE: Madagascar. Province uncertain: Ambohimombo forest (Tanala), 1,350–1,440 m, 22 Dec. 1894 (fr), *Forsyth-Major 326* (holotype, K).

Monoecious treelet or small tree 2–3 m tall, the new growth sparsely pilose to yellowish velutinous-tomentose, the mature leafy stems tomentose or glabrate, 2–3 mm diam. Leaves opposite to subopposite, petiolate; petioles pilose to tomentose, 2–5 mm by 1.2–2 mm; lamina chartaceous, ovate, elliptic or oblong, 20–50 mm by 10–25 mm, the apex acute to abruptly acuminate, the base cuneate to broadly cuneate or obtuse, the secondary veins 4–6 pairs, making a 60–75° angle with the costa, the venation scarcely visible to 2° adaxially, visible to 3° abaxially, the surfaces glabrous, the margin slightly revolute, entire or frequently bearing a pair of small, acute glandular teeth in the apical portion. Inflorescence axillary or terminal, the flowers solitary. Androecious flowers axillary, in bud globose to obovoid, 3–4 mm diam., subglabrous, the apex bearing 4 obtuse tepals, the pedicel 12–27 mm by 0.5 mm, basally bracteolate, subglabrous; at anthesis deeply 4-fid, ca. 10 mm diam., the lobes spreading flat, each bearing a broad, truncate tepal ca. 2 mm wide internally near the apex; stamens 16–18, broadly deltoid to ovoid-obtuse, 1–2 mm long by 1.5–2 mm wide, the filament very short or sessile, the loculi confluent apically into a single crescentiform loculus, the connective thick, not prolonged, the internal receptacle surface glabrous. Gynoecious flower subglabrous externally, on a pedicel 20–25 mm by 0.8 mm; at anthesis discoid, flat to slightly concave, 5–6 mm diam., the surface bearing ca. 38 densely crowded, free sessile, 4–6-sided, columnar carpels 0.5 mm diam., interspersed with short, simple hairs. Mature fruiting receptacle enlarged, the torus 15–35 mm diam., bearing 15–25 carpels; carpels ovoid to ellipsoid, 7–8 mm by 4–5 mm, immersed basally in cupules for ca. $\frac{1}{2}$ their length, the mesocarp thin, fleshy, the endocarp thin, brown.

Distribution. Endemic to Madagascar (Fig. 26).

Habitat. The species is known primarily from south central Madagascar where it occurs in the montane *Tambourissa/Weinmannia* wet forest zone from ca. 900 to 1,500 m, but also extends up into the sclerophyllous forest zone from ca. 1,300 to 2,000 m.

MADAGASCAR. TULEAR: Mt. Itrafanaomby (Ankazondrano) and its SW contreforts (high Mandrare basin), rain forest and ericoid scrub on gneissic crests, 1,600–1,963 m, end Dec. 1933 (fl), *Humbert 13518* (MO).

The species is most closely allied to *Ephippiandra myrtoidea*, from which it differs by its androecious flowers, which have more numerous stamens (16–18), and a single broad, truncate tepal on the inner extremity of each receptacle lobe.

EXCLUDED SPECIES

Ephippiandra capuronii Cavaco, Bull. Soc. Bot. France 104: 610. 1957 (= *Tambourissa beanjadensis* Lorence, see discussion under this species).

Tambourissa Sonn., Voy. Ind. Orient. ed. 1, 3: 267, tab. 134. 1782; ed. 2, 4: 405, tab. 134. 1806; Gmel., Syst. Nat. 2(1): 16. 1791, 'Tamburissa' (sphalm.); A.DC., Prodr. 16(2): 658. 1868; Baill., Hist. Pl. ed. 1, 1: 341. 1869; ed. 2, 1: 332. 1871; Baker, Fl. Mauritius 287. 1877; Benth. & Hook., Gen. Pl. 139. 1883; Pax, Pflanzenfam. 3(2): 101. 1899; Cordem., Fl. Réunion 300. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 66. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 39. 1911; Perk., Gatt. Monim. 44. 1925; Cavaco, Bull. Soc. Bot. France 104: 284. 1957; Cavaco in Humbert, Fl. Madagascar 80: 18. 1959; Hutch., Gen. Fl. Pl. 1: 118. 1964. TYPE: *T. quadrifida* Sonn.

Tamboure cissa Flacourt, Hist. Madagascar 133, pl. 69. 1661 (pre-Linnaean polynomial).

Mithridatea Comm. ex Schreb., Gen. Pl. 2: 783. 1791; Willd., Sp. Pl. 1(1): 27. 1797; Spreng., Syst. 5(3): 866. 1826, nom. nov. for *Tambourissa* Sonn.

Ambora Juss., Gen. Pl. 401. 1789; Juss., Ann. Mus. Hist. Nat. (Paris) 14: 130. 1809; Poir., Encycl. 7: 565. 1806; Tabl. Encycl. 784. 1806; Steud., Nom. Bot. 37. 1821; Endl., Gen. Pl. 4(2): 56. 1842; Tul., Ann. Sci. Nat. (Paris) 4(3): 29. 1855; Tul., Monogr. Monim. 295. 1855, nom. nov. for *Tambourissa* Sonn.

Schrameckia Danguy, Bull. Mus. Hist. Nat. (Paris) 28: 249. 1922; Perk., Gatt. Monim. 45. 1925; Metay,

Arch. Bot. Bull. Mens. 3(11): 177. 1929; Cavaco, Bull. Soc. Bot. France 105: 39. 1958. TYPE: *S. madagascariensis* Danguy (= *Tambourissa floribundata* Cavaco).

Phanerogonocarpus Cavaco, Bull. Soc. Bot. France 104: 612, figs. 1–4. 1957; Cavaco in Humbert, Fl. Madagascar 80: 2, fig. I:1–6. 1957, synonym. nov. TYPE: *P. capuronii* Cavaco (= *Tambourissa longicarpa* Lorence).

Small to moderate sized monoecious or dioecious trees, treelets or shrubs, $\pm$ aromatic. Leaves simple, usually opposite and decussate, rarely clustered into pseudovercels, or ternate to alternate, glabrous or pubescent with simple, rarely fasciculate, unicellular trichomes, the margin entire to serrate-dentate with glandular teeth, the venation festooned brochidodromous, the juvenile and sucker leaves usually heterophyllous, apically serrate-dentate. Inflorescence terminal, axillary, ramiflorous or cauliflorous, sometimes leafy, the axes bracteolate, the flowers solitary, fasciculate or disposed in dichasia, pleiochasia or thyrses; flower in bud fleshy, globose, globose-depressed, cylindrical to obovoid, urceolate or napiform (the gynoecious bud usually flattened or depressed apically), apiculate, the apex with several pairs of minute decussate tepals extending into the orifice; male receptacle at anthesis usually splitting into (3–)4–6(–7) $\pm$ regular, valvate segments, these remaining partially closed or usually spreading flat and $\pm$ reflexing; stamens eglandular, few to very numerous, multiseriate, situated on the glabrous or rarely hairy internal receptacle surface, the anthers tetrasporangiate, bilocular, the 2 loculi free and lateral, connivent, or confluent apically or rarely basally, longitudinally dehiscent, extrorse, sessile or with a distinct filament, the connective sometimes prolonged apically; pollen inaperturate, spheroid to ovoid, the sexine striato-reticulate to rugulate, granulate or granular-tectate; female receptacle at anthesis cylindrical, napiform, cupuliform or rarely discoid, the orifice generally 4(–10)-lobed or entire, the lobes reflexing or not; carpels numerous, immersed in and fused with the receptacle wall, the styles free and protruding, setose or conical to columnar, the internal receptacle surface frequently bearing simple hairs, in some species producing a copious mucilaginous exudate, the ovary unilocular, the ovule solitary, pendulous, anatropous to amphitropous. Fruiting receptacle cupuliform, subglobose, urceolate or cylindrical, corky brown externally, the fruiting carpels (drupes) enclosed within the accrescent receptacle wall which splits open irregularly

at maturity; carpels ovoid-compressed, surrounded by a fleshy, oily red-orange mesocarp, the endocarp horny, whitish to black, the surface smooth or variously sculptured, the embryo straight, the cotyledons flat, oval to elliptic. Gametic chromosome number: $n = 19$.

Distribution. *Tambourissa* is a genus of about 43 species restricted to the southwest Indian Ocean islands of Madagascar (26 spp.), the Comores (5 spp.), the Mascarene Islands of Mauritius (10 spp.), and Réunion (2 spp.). The species display a high degree of endemism, each being restricted to a given island and frequently to a specific habitat within the island.

Habitat. Species of *Tambourissa* are occasional to locally common components of evergreen moist, wet, and cloud forest formations, often conspicuous because of their peculiar flowering and fruiting receptacles.

TAXONOMIC HISTORY OF *TAMBOURISSA*

The name *Tambourissa*, adopted from the pre-Linnaean polynomial "Tamboure cissa" (presumably derived from "tamboul," a Malagasy term for testicles) employed by Flacourt (1661), was first validly published by Sonnerat in 1782. Sonnerat based his genus *Tambourissa* on a single species, *T. quadrifida*, which he undoubtedly described and illustrated while in Mauritius (Ly-Tio-Fane, 1976). A genus characterized by peculiar, often large, cupuliform or urceolate to cylindrical fruiting receptacles containing numerous immersed carpels, *Tambourissa* goes by the colorful local appellations of "Bois tambour" (drumwood) or "Pot de chambre jacot" (monkey's chamber pot) in Mauritius. In neighboring Réunion it is called "Bois de bombarde" (bombardment wood) because the ripe fruiting receptacle splits open irregularly to reveal an array of numerous, red-orange carpels set against the pale orange receptacular pulp (Fig. 17B). In Anjouan and Grand Comore (Comore islands) *Tambourissa* is known as "M'bweza," meaning to calm or sooth the pain, because its leaves are used medicinally in tea. Many species in Madagascar and Mayotte (Comores) go by the name of "Ambora." The species in Mohéli is called "Diarou."

Sonnerat felt the genus occupied a position somewhere between *Ficus* and *Dorstenia* because of its closed, fig-like buds and gynoeceous floral receptacle with an inferior, syncarpous gynoeceum. In 1789, the genus was redescribed by A. L. de Jussieu as *Ambora* from the Malagasy

vernacular name, and again as *Mithridatea* by Commerson, Sonnerat's mentor, in Schreber (1791). It is unclear why these authors redescribed *Tambourissa* under other names, because both genera were based on Sonnerat's original species, *T. quadrifida*. It was not until 1855 that Tulasne correctly placed the genus in Monimiaceae, publishing 11 new species of *Ambora* (1855a) for his monograph of the family (1855b).

In 1868, Alphonse de Candolle transferred all of Tulasne's species to *Tambourissa*, describing no new taxa but providing one new name. Baker (1877) described two new species of *Tambourissa* from Mauritius in his treatment of the family for "Flora of Mauritius and the Seychelles" and later described three more from Madagascar. At the turn of the century, Perkins and Gilg (1901) monographed the entire family for Engler's "Pflanzenreich," providing a synoptic treatment for *Tambourissa* and describing one new species. In her revision of the family ten years later, again for the "Pflanzenreich," Perkins (1911) published four additional species from the Comores and Madagascar. During this same period, Drake del Castillo (1902) published two new species, and Danguy (1922) published another (as *Schrameckia* because of its few, large stamens), all from Madagascar. After a hiatus of some 35 years, Cavaco revised the Malagasy Monimiaceae for "Flore de Madagascar et des Comores" (1959), publishing nine new Malagasy species of *Tambourissa* (1957a, 1957c, 1957d, 1957e, 1958c). Most recently, Lorence (1982) published seven new species and one subspecies of *Tambourissa* from the Malagasy region. *Phanerogonocarpus*, described by Cavaco (1957c), was named for its narrowly winged, tubular gynoeceous flowers and fruits and based on two Madagascan species. In the present revision of *Tambourissa*, three new names are proposed, and at the same time nine other taxa are reduced to synonymy.

GENERIC DELIMITATIONS AND SYSTEMATIC POSITION OF *TAMBOURISSA*

The genus *Phanerogonocarpus* was described by Cavaco (1957b) on the basis of its winged or ribbed, narrowly obconical to cylindrical gynoeceous flowering and fruiting receptacles (Fig. 17A), which he compared to the ribbed flowers of *Schrameckia*. Cavaco (1959) later undermined this character when he reduced *Schrameckia* to synonymy under *Tambourissa*. Furthermore, two species of *Tambourissa*, *T. perrieri*, and *T. quad-*

rifida, both possess ellipsoid to obovoid gynoecious floral receptacles approaching those of *Phanerogonocarpus*, although not as narrow. Carpels of both genera are identically immersed in and united with the receptacle wall (Figs. 13E, 16A–D). Furthermore, styles of *Phanerogonocarpus* are conical with an acute apex, possess an oblique styler canal, and are interspersed with short simple hairs as in *Tambourissa* (Fig. 16D).

Fruiting receptacles of both genera are externally corky brown and split open irregularly at maturity to reveal the numerous ripe carpels immersed in a pale orange matrix. That the fruit of *Phanerogonocarpus* splits lengthwise leaving the central tube more or less intact is related to its elongated shape; the ellipsoid to obovoid fruits of *Tambourissa quadrifida* behave similarly. Mature fruiting carpels of both genera consist of a bright orange, fleshy mesocarp enclosing the dark brown, finely sculptured endocarp. Supposed differences between the genera in gynoecious floral and fruit morphology are clearly those of degree and fail to support generic segregation.

In his original description of *Phanerogonocarpus*, Cavaco (1957c) noted the resemblance of its androecious flowers and stamens to those of *Tambourissa*, except for the presence of tepals ("staminodes") on the inner tips of the receptacle lobes in the former. This feature is, however, shared with a number of *Tambourissa* species such as *T. comorensis*, *T. floricosata*, and *T. paradoxa* to name a few. Cavaco correctly interpreted the staminal morphology of *Phanerogonocarpus* as falling within the range of variability displayed by *Tambourissa*, however.

Pollen of *Phanerogonocarpus capuronii* (= *Tambourissa longicarpa*) is subspheroid to ovoid with a striato-rugulate sexine composed of short, compactly spaced finger-like elements. That of *P. perrieri* (= *T. alaticarpa*) is spheroid to subovoid with a rugulate sexine composed of more continuous elements than in *P. capuronii*. Sexinous patterns of both species are strikingly similar to those found in many *Tambourissa* species, e.g., *T. comorensis*, *T. cordifolia*, *T. ficus*, *T. floricosata*, and *T. quadrifida*. A survey of pollen from a range of *Tambourissa* species shows the genus to have sexinous sculpturing ranging from striato-reticulate or rugulate to granular-tectate, thus readily accommodating the patterns displayed by *Phanerogonocarpus* (Lorence et al., 1984).

Regarding inflorescence structure, the sexually mixed pleiochasium terminated by one or two

gynoecious flowers in *Phanerogonocarpus* (Fig. 17A) also occurs in a number of *Tambourissa* species, e.g., *T. hildebrandtii* and *T. perrieri*. Finally, leaf architecture of the two genera overlaps. Adult leaves of a number of *Tambourissa* species, e.g., *T. thouvenotii* and *T. trichophylla*, as well as juvenile and sucker leaves of many species are dentate, as are adult leaves of *Phanerogonocarpus*. I can find no obvious basis for maintaining *Phanerogonocarpus* as a distinct genus and therefore propose that it be reduced to synonymy under *Tambourissa*.

Tambourissa has attained the highest level of floral morphological specialization of all the Malagasy Monimiaceae in the subfamily Molinedioideae. Most species are characterized by a strong androecious/gynoecious floral dimorphism, have flowers of both sexes closed in bud, have highly reduced tepals, show a range of staminal specialization via reduction and, most significantly, the gynoecious flowers have their carpels immersed in and fused with the massively developed ovary wall, with the fruiting carpels likewise enclosed in the accrescent receptacle which splits open irregularly at maturity.

INTRAGENERIC RELATIONSHIPS

Tambourissa, with about 43 species, is the largest genus of Monimiaceae in the Old World. Its members often display extensive interspecific variation in floral morphology (color, size, shape, and number of parts), pubescence, leaf morphology, and other characters. Even species which are obviously closely related with respect to features such as foliar and gynoecious floral morphology may differ radically and inexplicably in other features such as androecious floral or staminal morphology. This happens frequently enough to render the establishment of meaningful subgeneric categories such as subgenera or sections impossible at present. I have, therefore, chosen to place the species into informal groups of morphologically similar taxa to facilitate their comparison, but no phylogenetic implications are intended by this sequence. Nine species groups are listed below, each followed by a discussion (refer also to Tables 5–7):

1. Group A. *Tambourissa thouvenotii*,
T. trichophylla, *T. uapacifolia*
- Group B. *Tambourissa decaryana*,
T. hildebrandtii, *T. hum-*

- bertii*, *T. nitida*, *T. nosybensis*
- Group C. *Tambourissa floricostata*,
T. parvifolia
2. Group A. *Tambourissa beanjaden-*
sis, *T. comorensis*, *T.*
crassa, *T. elliptica*, *T. lep-*
tophylla, *T. madagascari-*
ensis
- Group B. *Tambourissa kirkii*, *T.*
paradoxa
3. *Tambourissa capuronii*, *T.*
moheliensis
4. *Tambourissa gracilis*, *T.*
purpurea, *T. religiosa*
5. *Tambourissa amplifolia*,
T. cocottensis, *T. cordifo-*
lia, *T. pedicellata*, *T. tau*,
T. tetragona
6. *Tambourissa bathiei*, *T.*
sieberi
7. *Tambourissa perrieri*, *T.*
quadrifida
8. *Tambourissa alaticarpa*,
T. longicarpa
9. *Tambourissa castri-delphi-*
nii, *T. ficus*, *T. peltata*

Group 1. This is a group of Madagascan species with canescent to velutinous or tomentose stems, leaves, and inflorescences (Table 5). The inflorescence is usually a ramiflorous or axillary (rarely cauliflorous) pleiochasium, often sexually mixed and frequently terminated by a gynoeceous flower, or the flowers may be solitary. Long acute, subulate or deltoid bracteoles subtend the pedicels and floral axis. The androeceous flower splits open flat into 4(–5) segments, bears scattered hairs internally in many species, and has fairly numerous stamens, frequently with prolonged connectives. The urceolate, napiform or subglobose gynoeceous flower opens by a small four-lobed, X-shaped orifice in most, and the densely velutinous internal surface is lined with many shortly conical styles. In most species, an abundance of oil cells occurs in the floral ground tissue of both sexes.

Group 1A. This group is comprised of three species with densely pubescent, usually apically toothed, adult leaves (*Tambourissa thouvenotii*, *T. trichophylla*) and densely velutinous-tomentose mature stems (Table 5). *Tambourissa*

uapacifolia fits here on the basis of its dense pubescence, although its leaves are entire and the inflorescence is apparently unisexual.

Group 1B. Five species with entire leaves and sparsely pubescent to canescent adult leaves and stems comprise this group (Table 5): *Tambourissa decaryana*, *T. hildebrandtii*, *T. humbertii*, *T. nitida*, and *T. nosybensis*. Of these, *T. decaryana*, *T. humbertii*, and *T. nosybensis* show trends towards cauliflory and unisexual inflorescences.

Group 1C. The last group contains two species differing in having subglabrous mature growth and internally glabrous female flowers (Tables 5, 6). *Tambourissa floricostata* has few, large stamens and floral receptacles with longitudinal lateral ridges; it was formerly placed in *Schrameckia* (Danguy, 1928). In *T. parvifolia*, the leaves are small and sclerophyllous and the stamens slender with distinct filaments lacking prolonged connectives.

Group 2. This diverse group includes species from the Comores, Madagascar, and Réunion, some of which appear to be much more closely related than others (Tables 5, 6). Most have glabrous to sparsely pubescent mature growth and inflorescences. Varying degrees of reduction occur in the inflorescence, which ranges from a sexually mixed or unisexual pleiochasium to a fascicle or solitary flowers. Small deltoid bracteoles subtend the often long, slender floral axis and pedicels. Two subgroups can be distinguished.

Group 2A. This category consists of species with medium-sized to large, 4-fid androeceous flowers that open flat and contain numerous long stamens with separate or apically confluent loculi and scarcely or non-prolonged connectives (Tables 6, 7). The gynoeceous flowers are globose-depressed, closed in bud, internally $\pm$ glabrous with crowded, shortly columnar blunt styles, open by an X-shaped orifice, and produce a copious mucilaginous secretion in the two Réunion species (*Tambourissa crassa*, *T. elliptica*) and *T. beanjadensis* (Madagascar). In *T. madagascariensis* (Madagascar) and the Comorean species (*T. comorensis*, *T. leptophylla*) the orifice of the gynoeceous receptacle is entire, internally pubescent and remains open during the entire floral development, a condition which is probably highly specialized (P. Endress, pers. comm.). Styles of the two latter species are bluntly columnar and shortly conical, respectively.

Group 2B. This group consists of two Comorean species in which the androeceous flowers are

small and globular, splitting only slightly and remaining nearly closed (*Tambourissa kirkii*), or merely opening by a small apical pore lined with scale-like tepals (*T. paradoxa*) (Table 6). In both species stamens are fewer, smaller, and more acute than in Subgroup A and have separate, medial loculi and acute, prolonged connectives. Androecious flowers of *T. moheliensis* correspond well with this group, but because its gynoecious flowers differ markedly from the other members, it will be discussed under Group 3. Gynoecious flowers of *T. kirkii* have an entire, circular orifice like *T. comorensis* and *T. leptophylla*, thus linking it to Group 2A; those of *T. paradoxa* are unknown.

Group 3. Members of this group are characterized by comparatively large, brown napiform gynoecious flowers that are closed and apically depressed in bud, later opening by a four-lobed, X-shaped orifice (Table 6). Unlike Group 2, the floral ground tissue contains numerous dark brown, presumably tanniferous, idioblasts. Androecious flowers of *Tambourissa capuronii* (Madagascar) are large, split open flat into four lobes, and have numerous large stamens with elongated lateral loculi. Those of *T. moheliensis* (Comores) are much smaller than in the former species, only split slightly open at anthesis (as in Group 2B), and differ in having fewer stamens with loculi that unite basally into a U-shape. Its androecious flowers therefore link Group 2B with Group 3.

Group 4. This group is composed of three Madagascan species which are glabrous to subglabrous, ramiflorous shrubs or small trees, mostly with arching branches, and have characteristic terminal dichasia, condensed pleiochasia or solitary flowers (Tables 5, 6). The gynoecious flowers and fruit are terminal, whereas the androecious flowers are either lateral, axillary, or ramiflorous. Floral receptacles are small and globose, monomorphic in both sexes, and open by small apical pores flanked by minute tepals. The comparatively small ripe fruiting receptacles are smooth and dark reddish externally, not pale and corky brown as in most other species. *Tambourissa gracilis* and *T. purpurea* both have similar androecious flowers with short, sessile stamens having apically confluent, crescentiform loculi; gynoecious flowers of the former are unknown. Flowers of *T. religiosa* are somewhat larger with longer, shortly conical styles. Also, its stamens have distinct filaments and separate loculi. Gynoecious flowers of *T.*

purpurea produce a mucilaginous plug or "hyperstigma" which occludes the pore; it is not known if this phenomenon occurs in the other two species.

Group 5. This group of subglabrous to glabrous trees, treelets and shrubs includes the bulk of the Mauritian species (Tables 5, 6). *Tambourissa pedicellata* seems to be the least specialized member in view of its monoecy, variability of floral disposition and inflorescence structure, and particularly its monomorphic androecious and gynoecious flowers with shallowly subglobose to cupuliform receptacles, relatively few parts, shortly conical styles, and stamens with separate loculi and distinct filaments.

Other members of the group (*Tambourissa amplifolia*, *T. cocottensis*, *T. cordifolia*, *T. tau*, and *T. tetragona*) display variations on this theme with varying degrees of specialization in one or more features. Leaves of most species are moderately small, opposite and decussate, and have distinct petioles. Trends of specialization are towards macrophyllly (*T. amplifolia*, *T. tau*), clustering of the leaves into pseudovercils of two to four pairs (*T. tau*), winged stems (*T. tetragona*), and reduction in petiole length (*T. cordifolia*, *T. tau*). Modifications of the inflorescence tend towards reduction from pleiochasia to dichasia, and finally to fascicles and monochasia, towards a shortening of the pedicels and floral axis, and from ramiflory to (often basal) cauliflory.

Other apparent trends are towards greater floral dimorphism, towards larger flowers with more numerous parts (*T. cordifolia*), and towards staminal structural modifications such as fusion of the loculi apically (*T. amplifolia*), basally (*T. cordifolia*), or their extreme separation on lateral arms (*T. tau*). Gynoecious flowers display a greater deepening and closure (*T. cocottensis*, *T. tetragona*) or opening (*T. peltata*), modifications of the styles via elongation (*T. tau*) or shortening (*T. peltata*), and elaborate development of the receptacular lobes with bright coloration to enhance their attractive potential for pollinators (*T. cordifolia*, *T. peltata*). The latter two species are further specialized in being dioecious. Gynoecious flowers of *T. ficus* correspond to this group in spite of their gigantism. Because of the ternate leaves and androecious floral morphology, however, I have included *T. ficus* under Group 9.

Group 6. This group consists of two species of large, monoecious trees, i.e., *Tambourissa sieberi* (Mauritius) and *T. bathiei* (Madagascar).

Both have relatively small leaves, moderately to densely pubescent new growth and densely yellowish velutinous, cauliflorous inflorescences which are generally unisexual pleiochasia or thyrses (Tables 5, 6). The globose female receptacle opens by a small pore in *T. sieberi* (mature gynoeceious flowers unknown in *T. bathiei*), and is lined with numerous long, narrowly conical, generally coalescent styles. Androeceious flowers of both species are large and 4–5-fid with lobes that spread open flat and have numerous large stamens.

Group 7. Apparently related to Group 6, this category also contains two species not closely allied to other members of the genus: *Tambourissa quadrifida* (Mauritius) and *T. perrieri* (Madagascar). Both are glabrous cauliflorous trees with relatively small, opposite leaves, grow in relatively drier habitats, and produce numerous unisexual or sexually mixed pleiochasia or thyrses along most of the trunk (Tables 5, 6). Androeceious flowers of both species split deeply into four flat or strongly recurved segments and bear hundreds of short stamens. The ellipsoid to obovoid or obpyriform gynoeceious flowers open by a small, three- to four-lobed apical pore, are internally velutinous and contain hundreds of very short, basally ventricose styles. The mature fruiting receptacles of both are elongated with a small orifice, resembling those of Group 8.

Group 8. This isolated pair of Madagascan species, *Tambourissa alaticarpa* and *T. longicarpa*, formerly comprised the genus *Phaneronocarpus*. Both are pubescent, monoecious, cauli- to ramiflorous treelets of the eastern wet forest zone with large, dentate leaves (Tables 5, 6). The pubescent, sexually mixed (rarely unisexual) inflorescence consists of one or two (rarely three) terminal gynoeceious flowers with lateral clusters of relatively small androeceious flowers grouped along the floral axis, a feature shared with certain members of Groups 1 and 7. The stamens have distinct filaments, free loculi, and the connective may or may not be prolonged. Most distinctive of Group 8 are the slender, obovoid to cylindrical, narrowly ribbed or winged gynoeceious flowering and fruiting receptacles with a small orifice. Gynoeceious receptacles of *T. florcostata* (Group 1C) are also ribbed, however, and those of Group 7 are ellipsoid to obovoid, although not as narrow, with comparably small orifices. The conical to ventricose styles are interspersed with dense short hairs in both species,

and a mucilaginous exudate is apparently produced in *T. longicarpa*.

Group 9. Characterized by ternate to subternate adult leaves with prominent, highly organized and finely reticulate venation, this group consists of three species (Tables 5, 6), i.e., *Tambourissa castri-delphinii* (Madagascar), *T. ficus*, and *T. peltata* (both Mauritius). Flowers are produced either at the base of the trunk (*T. ficus*), or on the upper trunk and older branches (*T. peltata* and *T. castri-delphinii*). The highly reduced inflorescence ranges from a short, condensed pleiochasium or fascicle in the latter, to a two-flowered fascicle or monochasium in the other two species. The group also displays a trend towards dioecy.

Androeceious flowers of *Tambourissa ficus* are the largest in the entire genus, with five to seven incurved or spreading lobes bearing from 900 to 1,800 ligulate stamens with separate, lateral to unifacial loculi and a thick, prolonged connective. Androeceious flowers of *T. peltata* and *T. castri-delphinii* are considerably smaller, deeply split into four or five recurved lobes, and bear numerous thin, broadly deltoid subsessile stamens with connivent or confluent lateral loculi.

Gynoeceious flowers of *Tambourissa peltata* are highly specialized, flat and discoid with four to seven elaborate, spreading verrucose sterile lobes and numerous crowded, highly reduced, flat columnar styles which produce a copious mucilaginous exudate. Those of *T. castri-delphinii* have an X-shaped orifice and conical styles, similar to some species in Group 5. In *T. ficus* the gynoeceious flowers are huge and urceolate, splitting into numerous straight or inflexed lobes with a broad orifice, and contain ca. 1,000–2,000 setose styles. Apart from their great size, gynoeceious flowers of *T. ficus* are morphologically similar to those of species belonging to Group 5 and link the two groups.

In the following key I have attempted to utilize vegetative characters as far as possible. Although certain species with outstanding vegetative characters are identifiable even from sterile specimens (e.g., *Tambourissa tetragona* is the only species with winged stems), for the majority, complete collections consisting of leafy stems, androeceious and gynoeceious flowers, and fruits are essential for reliable identification. Unfortunately, a large number of species, especially those from Madagascar and the Comores, are known only from androeceious or gynoeceious

flowers or fruits, and this has imposed certain limitations on the construction of this key. Although I was unable to examine all the Madagascan material cited by Cavaco (1959), I have seen additional material not cited by him. All collections in the Exsiccata and virtually all those used to plot the distribution maps have been seen by me. The last five species in the taxonomic treatment (nos. 39–44) are imperfectly known and consequently have not been included in the key. See key cited on following pages.

1. **Tambourissa trichophylla** Baker, J. Linn Soc., Bot. 20: 240. 1884; Perk. & Gilg, Pflanzenr. 4, 101: 68. 1901; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911; Cavaco in Humbert, Fl. Madagascar 80: 24, fig. VII:8–9. 1959. TYPE: Madagascar. ("Central Madagascar," probably Tananarive or Fianarantsoa): without precise locality, 1882 (fl), *Baron* 1953 (lectotype, K, here designated).

Monoecious treelet or tree attaining 15 m tall and 15–20 cm D.B.H., the new growth densely pilose-tomentose, the hairs simple, pale yellowish to grayish, the mature leafy stems 2–4 mm diam., tomentose, the hairs $\pm$ matted. Leaves opposite to subopposite, petiolate; petioles tomentose, 4–10 mm by 1.5–2 mm; lamina chartaceous to subcoriaceous, oblong, narrowly oblong, narrowly obovate, lanceolate or rarely elliptic, (50–)70–195 mm by 20–52 mm, the apex shortly acuminate, shortly acute or rarely obtuse, the base obtuse to rounded, rarely acute, abaxially tomentose-hirsute, especially along costa and secondary veins, the trichomes curved, adaxially pilose when young, glabrescent, the secondary veins 3–5 pairs, making a 50–60° angle with the costa, the arches low and broad, the venation disorganized, obscure adaxially and visible to 2°, prominent abaxially and visible to 3°, the margin slightly thickened and revolute, ciliate, entire or usually serrate-dentate in the apical $\frac{1}{3}$ – $\frac{1}{4}$ of the lamina with 1–2 pairs of short, broadly deltoid teeth. Inflorescence ramiflorous on leafless nodes or axillary, a usually unisexual, sometimes leafy pleiochasium of 3–7 flowers, or the flowers solitary, the floral axis fulvous to grayish, velutinous-tomentose, 14–55 mm by 1.5–2 mm, subtended by several deltoid-naviculate bracteoles 1–2 mm long, the pedicels 3–5 mm by 1.5 mm,

each subtended by 1(–2) subulate velutinous bracteoles 4–5 mm long. Androecious flower in bud globose, 5–7 mm diam., hirsute, apiculate with several pairs of minute hirsute tepals; androecious flower at anthesis unknown (presumably deeply 4-fid with spreading lobes as in *T. thouvenotii*); stamens in bud ca. 100, ovoid-deltoid, 1.5–2 mm long by 0.8–1 mm wide, the loculi lateral, separate, occupying ca. $\frac{3}{4}$ total length of stamen, the filament short or sessile, the connective thick, slightly prolonged apically, the internal receptacle surface with clusters of hairs between the stamens. Gynoecious flower in bud solitary or occasionally in pleiochasia, 7–8 mm diam. by 5–6 mm long, subglobose-depressed, hirsute, apiculate with 4 minute deltoid tepals; at anthesis shallowly 4(–5)-fid, the lobes $\pm$ incurved, the small X-shaped orifice 2–3 mm diam., the styles ca. 100, conical, 0.6–0.8 mm long by 0.3–0.4 mm wide basally, $\pm$ ventricose, acuminate, the internal receptacle surface velutinous between the styles. Fruiting receptacle solitary on the smaller branches, shallowly cupuliform, 30–48 mm diam. by 30 mm long, the walls 13–15 mm thick, both surfaces pale corky brown, the orifice subentire, comprising ca. $\frac{1}{2}$ total diam. of the fruit, the scattered styles conical, 0.3–0.5 mm long and wide basally, the internal receptacle surface hirsutulous; pedicel and peduncle stout, 6–8 mm long by 7–12 mm diam., hirsutulous. Submature carpels 6–8 mm long, 4–5 mm wide, 3–4 mm thick, ovoid-compressed, the endocarp brown.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. The species is locally common and fairly widespread in the *Tambourissa/Weinmannia* wet forest zone in the eastern and central regions ranging from 800 to 1,500 m.

MADAGASCAR. TAMATAVE: Ankaraka, ca. 1,500 m, 28 Dec. 1944 (fl, fr), *Anon. sub Herb. Alaotra* 3073 (MAD); National Route no. 2 at 69 km E of Tananarive, Mandraka forest reserve, 1,400 m, 28 Oct. 1978 (fl), *Lorence* 1879 (MAD, MAU, MO); 30 Oct. 1978 (fl), *Lorence* 2034 (MAD, MO); (fl), *Lorence* 2035 (MAD, MO); La Mandraka, Sept. 1963 (st), *Morat* 7 (MAD); National Route no. 2 at ca. 20 km W of Perinet, 950 m, 29 Oct. 1978 (st), *Lorence* 2000 (MAD, MO). TANANARIVE: Andringitra Massif, Ambodigraiss Forest near Antsirabe (sic), 1,200 m, 12 Jan. 1945 (fr), *Anon. sub Herb. Alaotra* 2242 (MAD). PROVINCE UNCERTAIN: head of Ankafinka Valley, 16 Nov. 1965 (fr), *Rakotozafy* 266 (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, 1882 (fl), *Baron* 1975a

KEY TO THE SPECIES OF *TAMBOURISSA*

[N.B.: for Madagascar material also refer to descriptions of last four species (nos. 39–43), not included in this key].

- 1a. Mature leaves, petioles, and stems conspicuously pubescent (canescent, villous, or velutinous-tomentose).
- 2a. Gynoecious floral and fruiting receptacles narrowly obovoid-cylindrical, tubular, bearing 4–6 longitudinal ridges or narrow wings; Madagascar.
 - 3a. Leaves serrate-dentate with 9–10 pairs of narrow, acute teeth in apical $\frac{2}{3}$ of lamina; staminal connective not prolonged beyond anther; gynoecious flower at most puberulent, glabrescent 34. *T. alaticarpa*
 - 3b. Leaves strongly dentate with (1–)2–3 pairs of broad, deltoid teeth in apical $\frac{1}{3}$ of lamina; staminal connective prolonged beyond anther; gynoecious flower densely pubescent 35. *T. longicarpa*
- 2b. Gynoecious floral and fruiting receptacles subglobose to cupuliform, at most ellipsoid to obovoid or pyriform, unwinged (if bearing 2 or many low, rounded ribs, then receptacle globose or discoid); Madagascar, Mascarenes, Comores.
 - 4a. Inflorescence a robust, cauliflorous, velutinous thyse with 16–90 flowers; floral axis stout, 50–110 mm long; mature buds globose, 12–14 mm diam.; large tree, Mauritius 30. *T. sieberi*
 - 4b. Inflorescence and buds much smaller and sparser, a cauliflorous pleiochasium; large or small trees; Madagascar.
 - 5a. Mature leaves abaxially velutinous-tomentose, at least on margins, costa and major veins; leafy stems and petioles velutinous-tomentose.
 - 6a. Adult leaves entire, the apex obtuse to retuse; loculi of stamens bearing scattered hairs externally, the connective not prolonged 3. *T. uapacifolia*
 - 6b. Adult leaves with 1–8 pairs of teeth in apical half of lamina, the apex shortly acute to acuminate, rarely obtuse; loculi of stamens glabrous, the connective prolonged.
 - 7a. Lamina elliptic to broadly elliptic, 50–90 mm wide; arches of secondary veins high and narrow; petioles 10–20 mm long; floral pedicels 12–17 mm long; fruit distinctly pedicellate 2. *T. thouvenotii*
 - 7b. Lamina narrowly oblong to oblong or oblanceolate, 20–50 mm wide; arches of secondary veins low, broad; petioles 4–10 mm long; floral pedicels 3–5 mm long; fruit subsessile to sessile 1. *T. trichophylla*
 - 5b. Mature leaves at most puberulent abaxially; stems and petioles canescent to sparsely villous.
 - 8a. Lamina very lustrous adaxially, dull abaxially, the apex long acuminate 4. *T. nitida*
 - 8b. Lamina dull on both surfaces, the apex at most acuminate.
 - 9a. Apex of lamina very shortly acuminate to obtuse or retuse; gynoecious receptacle subglobose-napiform, not ribbed, the styles 1–1.5 mm long, strongly papillose in both flower and fruit; stamens with a very short, apiculate connective 5. *T. hildebrandtii*
 - 9b. Apex of lamina acuminate; gynoecious receptacle discoid, ribbed, the styles 0.4–0.6 mm long, not papillose; stamens with an acute, prolonged connective 0.5 mm long 6. *T. nosybensis*
- 1b. Mature leaves, petioles, and stems glabrous, or at most with rare, scattered hairs.
 - 10a. Adult leaves ternate, dissoclate or even subalternate, except rarely opposite in *T. castri-delphinii*.
 - 11a. Flowers in short pleiochasia or fascicles of (3–)4–9 flowers on a common axis, never solitary, the pedicels slender, 0.5–1 mm diam.; Madagascar, E coast, Manakara to Fort Dauphin 36. *T. castri-delphinii*
 - 11b. Flowers solitary or in pairs, never on a common axis, the pedicels stout, 1.5–4.5 mm diam.; Mauritius.

- 12a. Buds, pedicels, and new vegetative growth puberulent; inflorescence basally cauliflorous; stamens 900–1,800, 0.5–1 mm wide, the loculi separate, the thick, obtuse connective prolonged for $\frac{1}{4}$ – $\frac{1}{3}$ total length of stamen; gynoecious flower massive, urceolate, with 6–8 erect to incurved lobes, the styles 1,000–2,000, setose, 1.5–5 mm long 37. *T. ficus*
- 12b. Buds, pedicels, and new vegetative growth glabrous; inflorescence ramiflorous, rarely cauliflorous on top part of trunk; stamens 200–400, 1.5–3 mm wide, the loculi confluent apically or the connective only slightly prolonged; gynoecious flower flat and discoid with 4–7 broad, spreading-reflexed lobes, the styles 400–500, crowded, columnar, flat-topped, coalescent, 0.5 mm long 38. *T. peltata*
- 10b. Adult leaves strictly in decussate pairs, opposite or rarely subopposite.
- 13a. Leafy stems quadrangular, conspicuously winged; Mauritius, summit of Mt. Cocotte 27. *T. tetragona*
- 13b. Leafy stems terete or subterete, neither quadrangular nor winged.
- 14a. Leaf base strongly cordate and amplexicaul; dioecious shrubs 50–150 cm high; Mauritius, in *Philippia* heath formation or low scrub 29. *T. cordifolia*
- 14b. Leaf base acute to weakly cordate, not amplexicaul; larger treelets or trees; forests of Mauritius, Réunion, Madagascar, Comores.
- 15a. Leaves pseudovercillate, clustered in 2–4 pairs separated by long intervals.
- 16a. Stamens $\pm$ T-shaped with separate loculi; buds and flowers externally corky brown; styles setose, 2–3 mm long; orifice of gynoecious flower with 5–10 irregular incurved deltoid lobes 26. *T. tau*
- 16b. Stamens clavate with apically confluent loculi; buds and flowers not externally corky; styles shortly conical, 0.6–1 mm long; lobes of female receptacle 4, deltoid, $\pm$ erect 25. *T. amplifolia*
- 15b. Leaves regularly disposed in pairs along stem.
- 17a. Mature inflorescence externally glabrous (or corky), at most with rare scattered hairs, not conspicuously nor finely pubescent under dissecting microscope.
- 18a. Flowers large, solitary, and terminal on branches (rarely terminal on leafy cauliflorous shoots); buds and female receptacles 12–15 mm diam.; androecious flowers splitting into 4–5 lobes, opening to 40–50 mm diam.; dioecious trees or treelets; leaves large, thick, obtuse to retuse, the higher order venation (3° and above) obscure, when dry fragrant and often bright yellow-green; Réunion 14. *T. crassa*
- 18b. Flowers in dichasia or pleiochasia, rarely solitary or in fascicles of 2, either ramiflorous, axillary or terminal (if solitary, then buds and flowers much smaller, less than 9 mm diam.); leaves smaller and thinner, when dry not fragrant, dull dark green or brownish, not bright yellow-green; Mauritius, Réunion, Madagascar, Comores.
- 19a. Floral pedicel and peduncle acutely quadrangular, 5–7 mm long, bearing four rows of decussate ciliate bracteoles; buds and flowers externally corky brown, cauliflorous, solitary or in groups of 2; Mauritius, summit of Mt. Cocotte 28. *T. cocottensis*
- 19b. Floral pedicel and peduncle terete to subtetragonal, neither quadrangular nor with four rows of bracteoles; Mauritius, Madagascar, Réunion, Comores.
- 20a. Adult leaves small, coriaceous, 15–45 mm by 9–22 mm, obovate, elliptic or oblong, the apex obtuse to retuse; inflorescence ramiflorous on leafless stems, a lax, glabrous to canescent pleiochasia ca. 25–70 mm long; small monoecious trees; montane forests, central Madagascar 10. *T. parvifolia*

- 20b. Adult leaves mostly much larger, the inflorescence mostly exceeding 15 mm long; if leaves as small, then inflorescence axillary or terminal on leafy stems, a short, congested dichasium or pleiochasium 10–15 mm long, or the flowers rarely solitary; Madagascar, Mauritius, Réunion, Comores.
- 21a. Inflorescence and buds externally corky and pale brown; androecious buds 15–19 mm diam.; connectives of stamens acute, prolonged, with several hairs at apex; Madagascar ... 20. *T. capuronii*
- 21b. Inflorescence and buds externally smooth, dark brown or blackish, never corky; androecious buds 2–11 mm diam.; connectives of stamens prolonged or lacking, but never bearing hairs; Madagascar, Mauritius, Réunion, Comores.
- 22a. Inflorescence terminal or axillary, a short, congested dichasium or pleiochasium 10–15 mm long (flowers rarely solitary); Madagascar.
- 23a. Leaves larger, 70–150 mm by 30–60 mm; lamina coriaceous, the 3–5° veins prominent abaxially, a marginal fimbrial vein present; buds and flowers 7–10 mm diam. by 4–7 mm long; stamens 60–82, with distinct filament and separate loculi 21. *T. religiosa*
- 23b. Leaves usually much smaller, 40–85 mm by 15–40 mm; lamina subcoriaceous, the 3–4° veins not prominent, a marginal fimbrial vein absent; buds and flowers 3–5.5(–7) mm diam. by 2.5–6(–7) mm long; stamens 20–32, ± sessile, the filament not distinct, the loculi confluent apically into a single crescentiform loculus 22. *T. purpurea*
- 22b. Inflorescence rami- or cauliflorous, a lax, occasionally leafy, pleiochasium or thyrse greatly exceeding 15 mm long (flowers occasionally solitary, axillary); Mauritius, Réunion, Comores, Madagascar.
- 24a. Androecious receptacle splitting for less than half its length into 4–5 short, incurved or erect lobes, or opening by a small, subentire apical pore.
- 25a. Floral pedicels 15–66 mm long, glabrous; androecious receptacle shallowly 4–6-fid, the lobes lacking scale-like tepals internally; stamens with separate loculi; leaf apex shortly acuminate, acute, obtuse or retuse; Mauritius 24. *T. pedicellata*
- 25b. Floral pedicel 5–13 mm long, with scattered hairs; androecious receptacle with obtuse, scale-like tepals internally on the lobes or flanking the orifice; stamens with confluent loculi; leaf apex acute to long acuminate.
- 26a. Androecious flowers opening by a small, circular orifice 1–2 mm diam.; stamens ± sessile with apically confluent loculi; leaf apex acuminate; Madagascar 23. *T. gracilis*
- 26b. Androecious flower splitting into 4 shallow lobes; stamens with loculi confluent basally into a U-shape; leaf apex acute or rounded; Mohéli (Comores) 19. *T. moheliensis*

- 24b. Androecious receptacle deeply split at anthesis for more than half its length into (3-)4-5 deltoid lobes that ultimately spread open flat or reflex.
- 27a. Gynoecious receptacle longer than wide, obovoid to pyriform or ellipsoid; cauliflorous species; inflorescence a stout pleiochasium or thyrse 60-180 mm long; floral axis 2-4 mm diam.
- 28a. Leaves thin, chartaceous, slightly lustrous, the ultimate venation prominent and raised on both surfaces, the apex acuminate; orifice of gynoecious flower 3-4 mm diam. (ca. $\frac{1}{2}$ total width of receptacle); androecious buds globose; Madagascar 32. *T. perrieri*
- 28b. Leaves subcoriaceous, dull, the ultimate venation frequently obscure on both surfaces, the apex shortly acuminate to mucronate, obtuse, rounded or retuse; orifice of gynoecious flower 1-2 mm diam. (ca. $\frac{1}{4}$ total width of receptacle); androecious buds obovoid to ellipsoid; Mauritius, dry western forests 33. *T. quadrifida*
- 27b. Gynoecious receptacle as wide as or wider than long, subglobose to globose-depressed or napiform-depressed; ramiflorous species; inflorescence a slender pleiochasium 20-50 mm long; floral axis 1-1.5 mm diam. (if cauliflorous, then flowers solitary or in fascicles of 2-3).
- 29a. Floral axis 20-45 mm long; androecious buds distinctly apiculate; Madagascar.
- 30a. Lamina 34-47 mm by 18-28 mm; stamens 35-36, sessile, obtuse to deltoid, 0.6-1 mm long, the loculi apically confluent into a single crescentiform loculus; orifice of gynoecious flower closed in bud, at anthesis 4-lobed, X-shaped 11. *T. beanjadenensis*
- 30b. Lamina 42-80 mm by 24-34 mm; stamens ca. 200, lanceolate to subulate, 2.5-4 mm long, the loculi separate, lateral; orifice of gynoecious flower open in bud, at anthesis circular, entire 12. *T. madagascariensis*
- 29b. Floral axis 10-15 mm long (or in the flowers solitary); androecious buds not markedly apiculate; Réunion 13. *T. elliptica*
- 17b. Mature inflorescence canescent to velutinous-tomentose or strigillose with conspicuous, often fine and $\pm$ appressed hairs under dissecting microscope.
- 31a. Leaves highly lustrous adaxially, dull abaxially; Madagascar 4. *T. nitida*
- 31b. Leaves not markedly lustrous adaxially, dull on both surfaces; Madagascar, Mauritius, or Comores.
- 32a. Lamina macrophyllous, ca. 150-325 mm by 85-115 mm; gynoecious flowers in pleiochasia of 6-11, the pedicels 6-23 mm long, the receptacle napiform-depressed, 7-8 mm diam. by 4-5 mm long, the orifice X-shaped, 4(-5)-lobed, the lobes incurved with inner surface bearing 25-40 sterile appendages resembling styles but larger (androecious flowers unknown); Madagascar 7. *T. decaryana*
- 32b. Leaves smaller, or if as large then floral pedicels 25-60 mm long; female receptacle lobes lacking conspicuous style-like sterile appendages on inner surface (or gynoecious flowers unknown); Madagascar, Mascarenes, Comores.

- 33a. Androecious and gynoecious floral receptacles with 2-4 low, external longitudinal ridges 9. *T. floricosata*
- 33b. Androecious and gynoecious floral receptacles lacking 2-4 external ridges (numerous low ribs present in gynoecious flowers of *T. nosybensis*).
- 34a. Styles bearing long (1-1.5 mm), scattered hairs externally; gynoecious buds and flowers 15-20 mm diam.; Madagascar 8. *T. humbertii*
- 34b. Styles glabrous or, if bearing scattered hairs, these much shorter, 0.5 mm long (in *T. kirkii*, Anjouan); gynoecious buds and flowers 7-15(-16) mm diam.; Mauritius, Madagascar, Comores.
- 35a. Androecious receptacle remaining partly or almost completely closed at anthesis, either shallowly split or globose with subtire apical pore; stamens narrowly acute, tapering gradually to a slender, conspicuously prolonged connective; Comores.
- 36a. Androecious receptacle opening by a small apical orifice ca. 2 mm diam. flanked internally by several series of small, obtuse scale-like tepals; prolonged connectives slightly exerted from orifice; gynoecious flowers unknown; Anjouan. 18. *T. paradoxa*
- 36b. Androecious receptacle splitting into 3-4 shallow segments, lacking small, obtuse scale-like tepals internally; tips of staminal connectives not exerted from orifice; Anjouan, Mohéli.
- 37a. Staminal loculi separate; orifice of gynoecious receptacle circular, entire; Anjouan 17. *T. kirkii*
- 37b. Staminal loculi mostly united basally into a U-shape; orifice of gynoecious receptacle with 4 large deltoid lobes; Mohéli 19. *T. moheliensis*
- 35b. Androecious receptacle splitting more than halfway open, the lobes spreading flat or reflexing at anthesis, the staminal connectives only slightly or not prolonged (except in *T. moheliensis*); Mauritius, Madagascar, Comores.
- 38a. Mature floral pedicels 25-80 mm long.
- 39a. Lamina 250-430 mm by 80-230 mm; flowers either solitary, fasciculate, or in short pleiochasia of 3-7; androecious flowers at anthesis 14-18 mm diam.; stamens 1-1.5 mm long, the loculi apically confluent; slender, basally cauliflorous treelets; Mauritius 25. *T. amplifolia*
- 39b. Lamina generally much smaller; flowers in ample pleiochasia or thyrses of 7-34; androecious flowers at anthesis 20-35 mm diam.; stamens 2-3 mm long, the loculi separate (apically confluent in *T. bathiei*, Madagascar); larger trees; Madagascar, Comores.
- 40a. Orifice of gynoecious floral receptacle circular, entire, open even in bud; androecious buds 6-8 mm diam.; Mayotte (Comores) 16. *T. leptophylla*
- 40b. Orifice of gynoecious floral receptacle closed in bud, at anthesis splitting into a 4-lobed, X-shaped orifice with deltoid lobes; Comores, Madagascar.

- 41a. Gynoecious buds and flowers externally corky brown, nappiform, the apex strongly depressed; lamina 120–220 mm by 40–70 mm; Mohéli (Comores) 19. *T. moheliensis*
- 41b. Gynoecious buds and flowers externally fulvous velutinous-canescens, globose, the apex apiculate; lamina 40–58 mm by 20–25 mm; Madagascar 31. *T. bathiei*
- 38b. Mature floral pedicels 5–15 mm long.
- 42a. Leaves small, 14–45 mm by 9–22 mm, coriaceous, obovate or oblong, the apex obtuse to retuse; inflorescence puberulent or sparsely canescent; montane forests of central Madagascar 10. *T. parvifolia*
- 42b. Leaves much larger, generally exceeding 50 mm long, if apex retuse or obtuse, then inflorescence villous-tomentose; Madagascar, Comores.
- 43a. Gynoecious receptacle open even in bud, the orifice circular and entire; Comores.
- 44a. New stems and leaves glabrous; inflorescence a short pleiochasium of 4–9 flowers; mature androecious buds 9–14 mm diam.; stamens 125–150; gynoecious flowers and fruit with short, bluntly columnar styles ca. 0.5 mm long; gynoecious floral orifice ca. $\frac{1}{2}$ – $\frac{2}{3}$ total diam. of receptacle; fruit smooth, mottled reddish brown, the orifice ca. $\frac{1}{3}$ – $\frac{1}{2}$ total diam. of receptacle; Grande Comore 15. *T. comorensis*
- 44b. New stems and leaves finely pubescent; inflorescence a lax pleiochasium or thyrses of (5–)7–25 flowers; mature androecious buds 6–8 mm diam.; stamens ca. 80–90; gynoecious flowers and fruit with sharply acute, conical styles ca. 0.6–1 mm long; gynoecious floral orifice ca. $\frac{1}{4}$ – $\frac{1}{3}$ total diam. of receptacle; fruit uniformly dull, corky brown, the orifice ca. $\frac{1}{6}$ – $\frac{1}{4}$ total diam. of receptacle; Mayotte 16. *T. leptophylla*
- 43b. Gynoecious receptacle closed in bud, at anthesis splitting into 4 shallow lobes, the orifice X-shaped; Madagascar.
- 45a. Apex of lamina shortly acuminate to obtuse or retuse; gynoecious receptacle subglobose to nappiform, not ribbed externally, the styles 1–1.5 mm long, strongly papillose in flower and fruit; stamens with a very short, apiculate connective; Madagascar 5. *T. hildebrandtii*
- 45b. Apex of lamina long acuminate; gynoecious receptacle discoid, externally many-ribbed, the styles ca. 0.4–0.6 mm long, not papillose; stamens with an acute, prolonged connective ca. 0.5 mm long; Nosy-Be island (NW Madagascar) 6. *T. nosybensis*

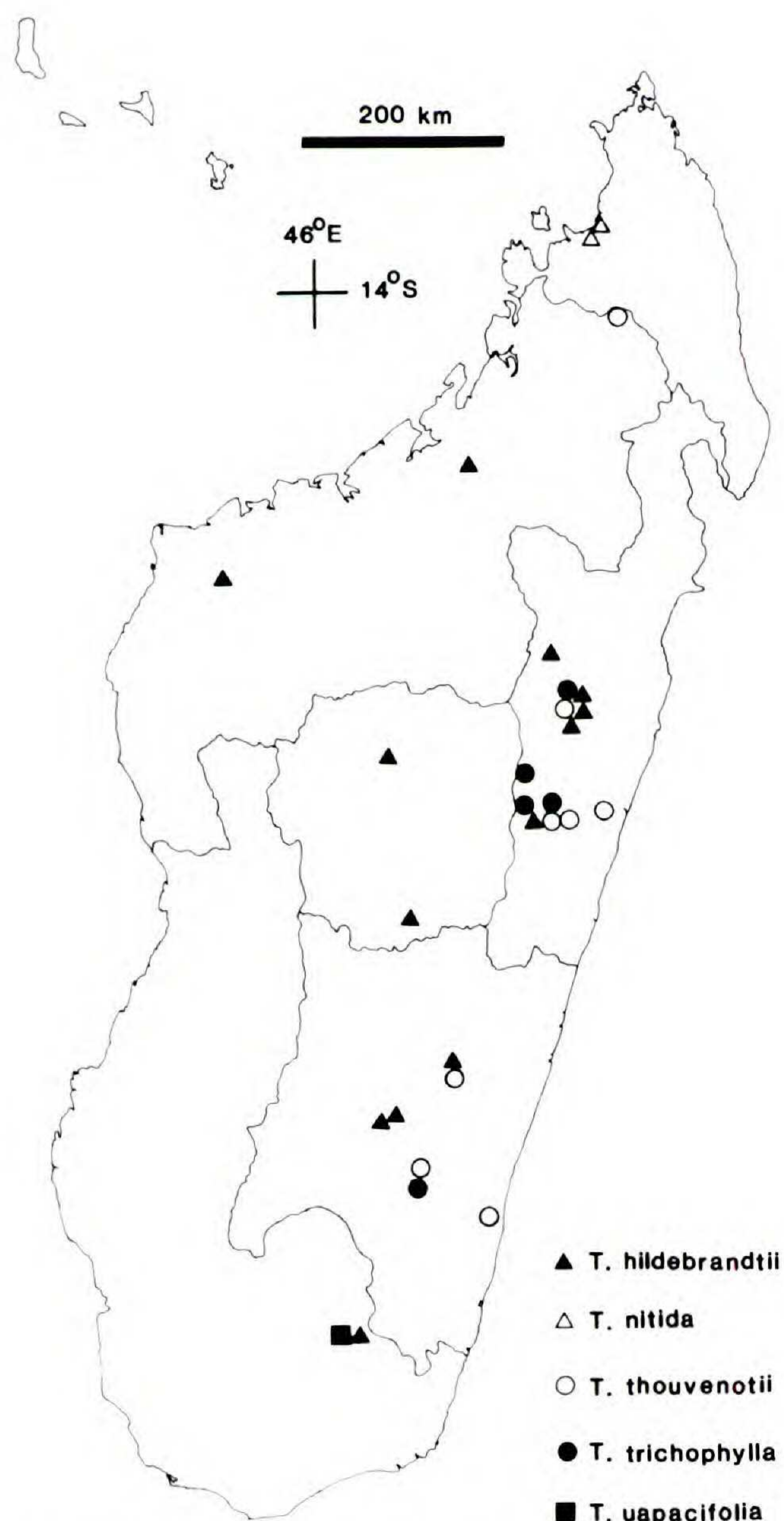


FIGURE 27. Distribution map of some *Tambourissa* species in Madagascar.

(K, syntype); Dec. 1883 (st), *Baron 2243* (K); (fl), *Baron 2994* (BM, K); 1885 (fl), *Baron 3433* (K); Feb. 1882 (st), *Parker s.n.* (K).

Tambourissa trichophylla and its close ally, *T. thouvenotii*, are both characterized by apically dentate adult leaves. This character may represent a state of neoteny, as it occurs in young plants and sucker shoots of many other *Tambourissa* species. *Tambourissa trichophylla* is distinguishable from *T. thouvenotii* by its narrower oblong leaves with fewer and broader teeth (only 1–3 pairs), its more widely spaced secondary veins with lower, stronger arches, its sparser and more curved trichomes, and its smaller flowers with much shorter pedicels and longer bracteoles. Both species remain distinct where they occur sympatrically and both belong to species Group 1A.

Vernacular name. Ambora saha (Madagascar).

2. *Tambourissa thouvenotii* Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 28: 250. 1922. TYPE: Madagascar. Tamatave: Analamazaotra (Perinet), ca. 1919 (fl), *Thouvenot 109* (lectotype, K, here designated; isoelectotypes, P, 2 sheets).

T. trichophylla Baker var. *thouvenotii* Cavaco in Humbert, Fl. Madagascar 80: 25, fig. VII:1–4. 1959.

Monoecious or subdioecious treelet or tree 8–22 m tall and 15 cm or more D.B.H., the new growth densely velutinous, the trichomes simple, yellowish, the mature leafy stems velutinous, 3–5 mm diam. (sucker stems to 12 mm diam.). Leaves opposite, petiolate; petioles velutinous, 10–20 mm by 2–3 mm; lamina subcoriaceous, broadly elliptic to elliptic, rarely broadly oblong, ovate or obovate, (70–)85–185 mm by (37–)50–90 mm, the apex shortly acuminate, rarely obtuse, the base obtuse to rounded, the young lamina adaxially pilose, glabrescent except on costa and major veins, abaxially densely velutinous with soft, straight yellowish hairs, the secondary veins 4–7 pairs, making a 35–50° angle with the costa, the arches high and narrow, the venation obscure adaxially and visible to 2°, prominent abaxially and visible to 4°, the margin slightly thickened and revolute, ciliate, the apical $\frac{1}{3}$ – $\frac{2}{3}$ of the lamina usually serrate-dentate with 1–8 pairs of short teeth. Inflorescence cauliflorous, ramiflorous or axillary, a sexually mixed or unisexual pleiochasium of 3–7 flowers, or the flowers rarely solitary, the floral axis velutinous, 25–57 mm by 2–3 mm, subtended by several velutinous, deltoid-subulate bracteoles 2–3 mm long. Androecious flower in bud globose, 10–12 mm diam., hirsute-velutinous, apiculate with several minute, velutinous tepals, the pedicel 12–17 mm by 1.5–2 mm; at anthesis deeply 4-fid, 12–25 mm diam., the lobes spreading flat; stamens numerous, ca. 50–100, deltoid-lanceolate to subulate, 3–7 mm long by 1–1.5 mm wide, slightly incurved, the filament short or sessile, the loculi lateral to slightly unilateral, separate, occupying $\frac{2}{3}$ – $\frac{3}{4}$ total length of the stamen, the connective prolonged apically, acute, the internal receptacle surface pubescent. Gynoecious flower in bud broadly napiform-depressed, 11–13 mm diam. by 6–7 mm long, velutinous, apiculate with several minute tepals, the pedicel 6–10 mm long; at anthesis shallowly and irregularly 5–6-lobed,

the orifice 3–4 mm diam., the lobes incurved, not reflexed; styles numerous, ca. 100–150, very shortly conical, 0.3 mm long by 0.2 mm wide basally, the apex acuminate to acute, the internal receptacle surface velutinous between the styles. Fruiting receptacle solitary on old branches, irregularly cupuliform, 40–100 mm diam. by 32–55 mm long, the walls 12–18 mm thick, both surfaces corky, reddish brown, externally hirsute-velutinous, the orifice subentire, comprising $\frac{1}{4}$ – $\frac{1}{2}$ total width of the fruit; styles numerous, shortly conical, 0.3–1.6 mm long by 0.3–0.5 mm wide basally; pedicel and peduncle 15–50 mm long by 9–15 mm wide. Mature carpels 15–16 mm long, 6–7 mm wide, 4–5 mm thick, the endocarp light brown, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa thouvenotii* is fairly widespread and often locally common in the *Tambourissa/Weinmannia* montane wet forest zone of the eastern and central regions from ca. 800 to 1,400 m. In addition to the obvious morphological differences, both *T. thouvenotii* and *T. trichophylla* appear to occur sympatrically in at least some areas, e.g., Massif d'Andringitra (Anon. sub Herb. Alaotra 2242, MAD; Anon. sub Herb. Alaotra 2311, MAD), where they remain distinct.

MADAGASCAR. MAJUNGA: Circagri Bealanana (near Tsaratanana massif), June 1953 (st), Anon. sub Agronomic Service s.n. (MAD). FIANARANTSOA: Ampamherana, Fianarantsoa, 24 Nov. 1949 (fl), Anon. sub SF 1248 (MAD); Andringitra Massif, Ambatapaiso near Antsirabe (sic), 12 Jan. 1945 (st), Anon. sub Herb. Alaotra 2311 (MAD); in rain forest, Tsararano, Vondrozo district (E coast, near Farfangana), Dec. 1963 (fl), Bosser 18583 (MAD). TAMATAVE: Ranomafana East, 300–400 m (fr), Chebonis s.n. (MAD); Analamazaotra Forest (near Perinet), Jan. 1919 (fl), Anon. sub SF 73 (probably a syntype, MAD); National Route no. 2 at 1 km W of Perinet, ca. 900 m, 29 Oct. 1978 (st), Lorence 2014 (MAD, MAU, MO); (st), Lorence 2015 (MAD, MAU, MO); Perinet, 950 m, 13 Aug. 1968 (st), McWhirter 121 (K); Analamazaotra, (fl), Thouvenot 73 (K, P, syntypes); 1919 (fl), Thouvenot s.n. (BM); Andovoranto Province, Moramanga District, Analamazaotra Forest, 950 m, 3 Nov. 1912 (st), Viguiet & Humbert 1106 (G); Ambatondrazaka (fl), Anon. sub SF 2548 (MAD). WITHOUT PRECISE LOCALITY: North Madagascar, 1892 (fr), Baron 6721 (K).

Tambourissa thouvenotii seems most closely related to *T. trichophylla*, which also possesses dentate-serrate adult leaves. It is distinguishable from the latter species by its much larger, broader and usually elliptic leaves with more numerous

teeth (up to 8 pairs) and more closely spaced secondary veins with higher and weaker arches showing a tendency to become almost craspedodromous (Fig. 7A). *Tambourissa thouvenotii* also has a denser, more yellowish indument of straight hairs, much longer floral pedicels, shorter bracteoles, and larger flowers than does *T. trichophylla*. Both species are closely allied to *T. uapacifolia* which also belongs to species Group 1A.

Vernacular names. Ambora, Ambora bera-vina (Madagascar).

3. *Tambourissa uapacifolia* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 351. 1957; Cavaco in Humbert, Fl. Madagascar 80: 24, fig. V:6–7. 1959. TYPE: Madagascar. Tulear: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, 14–15 Nov. 1928 (fl, fr), Humbert 6604 (holotype, P; isotypes, P, 2 sheets).

Monoecious tree, the new growth densely velutinous, the mature leafy stems 4–5 mm diam., velutinous-hirsute. Leaves opposite to subopposite, petiolate; petioles 5–16 mm by 1.5–2.5 mm, velutinous; lamina subcoriaceous, obovate to elliptic, 65–155 mm by 20–85 mm, hirsutulous when young, later glabrescent except abaxially on the major veins and margin, the apex obtuse or rarely shortly acute, the base acutely cuneate, rarely obtuse, the secondary veins 4–6 pairs, making a 40–50° angle with the costa, the venation depressed and visible to 3° adaxially, raised and visible to 4° abaxially, the margin thickened, slightly revolute, ciliate. Inflorescence cauliflorous or ramiflorous on leafless nodes, a velutinous, pendulous unisexual (always?) pleiochasium of 5–9 flowers, the floral axis 20–55 mm by 1.5–2 mm, subtended by small, naviculate bracteoles 1.5–2 mm long. Androecious flower in bud globose, 6–10 mm diam., velutinous, apiculate, the apex with several pairs of small, hirtellous-velutinous tepals, the pedicel velutinous, 10–17 mm by 1–1.5 mm; at anthesis 4-fid; 17–20 mm diam., stamens ca. 100–300, clavate, 1–2 mm long by 0.6–1 mm wide, the filament comprising ca. $\frac{1}{3}$ – $\frac{1}{2}$ the total length, the loculi lateral, separate or confluent apically, $\pm$ parallel, comprising ca. $\frac{1}{2}$ – $\frac{2}{3}$ total length of the stamen, the connective not prolonged, the external surface of loculi bearing medially several scattered simple hairs, the internal receptacle surface bear-

ing scattered simple hairs between the stamens. Gynoecious flower unknown. Fruiting receptacle solitary on older leafless stems, the submature fruit cupuliform, 35–41 mm diam. by 20–27 mm long, the orifice ca. 10–15 mm diam., subentire, the walls 14–16 mm thick, externally pale corky brown with scattered hairs, the internal surface hirsute, the styles scattered, broadly conical, 0.5–0.6 mm long by 0.6–0.8 mm wide basally; pedicel and peduncle hirsute-velutinous, 25–50 mm long by 3–4 mm diam.; submature carpels 9–12 mm long, 7–8 mm wide, 5–6 mm thick, the endocarp light brown, the surface foveolate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa uapacifolia* is currently known from three collections. The type is from southeastern Madagascar at 1,000 to 1,400 m, presumably in *Tambourissa/Weinmannia* wet forest where Humbert also collected *T. capuronii* and *T. hildebrandtii*. The other two collections are from near Moromanga, probably in the same vegetation type. Additional collections and field data are obviously needed.

MADAGASCAR, TAMATAVE: S of Moromanga, 9 Feb. 1930 (fl), *Decary 7042* (P); Moromanga to Andasibe (Perinet), pk 51, 26 Oct. 1953 (fr), *Anon. in SF-7805* (P).

Tambourissa uapacifolia belongs to species Group 1A, which also includes *T. trichophylla* and *T. thouvenotii* (for which Humbert apparently mistook it). It is distinguishable from the previous two species by its larger and laxer inflorescence with longer floral pedicels, smaller bracteoles, stamens with scattered hairs on the loculi, unprolonged connectives, and by its obtuse leaves with entire margins resembling those of certain species of *Uapaca* (Euphorbiaceae).

4. ***Tambourissa nitida*** Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 34: 280. 1928; Cavaco in Humbert, Fl. Madagascar 80: 25. 1959. TYPE: Madagascar. Diego Suarez: S of Biramanja (Ambilobe), ca. 1927 (fl, fr), *Ursch 267* (holotype, P; isotype, P).

Small tree attaining 6 m tall, the new growth pilose-hirsute, the mature leafy stems 1.5–4.5 mm diam., blackish brown, hirsutulous. Leaves glabrous, opposite, petiolate; petioles 10–16 mm by 1–1.5 mm; lamina chartaceous to subcoriaceous, ovate to narrowly ovate, elliptic, rarely oblong, 60–110 mm by 26–40 mm, the apex long

acuminate, $\pm$ recurved, the base acutely decurrent, the secondary veins 6–9 pairs, making a 60–70° angle with the costa, the venation prominent on both surfaces, visible to 3° adaxially and to 4° abaxially, the adaxial surface highly lustrous, the abaxial surface dull, the margin slightly revolute. Inflorescence axillary, a sexually mixed pleiochasium of 3–5 flowers, or the flowers solitary, the axes hirsute-canescens with pale, simple hairs; floral axis 5–12 mm by 1 mm, subtended by several subulate-naviculate, hirsute bracteoles 1.5–2 mm long. Androecious flower in bud globose, 6–7 mm diam., sparsely pubescent, apiculate with 3–4 narrowly deltoid, hirsute tepals, the pedicel 3–4 mm by 1–1.5 mm, subtended by a bracteole; androecious flower at anthesis unknown; stamens in bud ca. 60, ellipsoid to clavate, 1–1.5 mm long by 0.5 mm wide, the loculi separate, lateral, occupying ca. $\frac{1}{2}$ total length of the stamen, connivent at the obtuse apex, the connective not prolonged, the internal receptacle surface with scattered groups of simple hairs between the stamens. Gynoecious flower at anthesis unknown, in bud turbinate or napiform, 6.5–8 mm diam. by 4–5 mm long, usually with two low, basal longitudinal ridges, externally hirsutulous-canescens, apiculate with 3–4 acute tepals; styles numerous, ca. several hundred, conical or clavate, 0.7–0.9 mm long by 0.3 mm diam., medially ventricose, the apex abruptly acuminate, the internal receptacle surface velutinous, the hairs slightly shorter than the styles. Mature fruiting receptacle unknown. Immature mal-formed fruit axillary on the leafy stem, $\pm$ napiform, ca. 15 mm diam., externally blackish and corky brown, pubescent, the internal surface hirsute, the scattered styles broadly conical, tapering to an acuminate apex, 0.5–0.6 mm wide by 0.8–1 mm long; pedicel and peduncle stout, obconical, 10–12 mm long by ca. 5 mm diam. medially. Carpels unknown.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa nitida* is only known from two collections, both from the Sambirano region of Diego Suarez near the northern tip of Madagascar. The area where both collections originated appears to represent a transition zone between wet and deciduous forest.

MADAGASCAR, DIEGO SUAREZ: Ifazy Valley, Aug. 1909, *Perrier de la Bâthie 10126* (P).

Tambourissa nitida belongs to species Group

1B. Although the slight ridges on the female receptacles are reminiscent of *T. floricostata*, *T. nitida* is easily distinguishable because of its adaxially lustrous leaves with long acuminate, recurved apices. Also, its gynoeceous flowers are more densely velutinous internally and its stamens lack the prolonged connectives of most allied species. Mature flowers, fruiting receptacles, as well as the habitat of this remarkable species are unknown.

5. *Tambourissa hildebrandtii* Perk. in Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18:N-P. 1901; Perk., Gatt. Monim. fig. 34:N-P. 1925; Cavaco in Humbert, Fl. Madagascar 80: 29. 1959. TYPE: Madagascar. Tananarive: North Betsileo (Ant-) Sirabe, Aug. 1880 (fl), *Hildebrandt* 3563 (lectotype, K, here designated; isoelectotypes, BM; G, 2 sheets; P, 2 sheets).

T. baroni Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911; Cavaco, Bull. Soc. Bot. France 104: 284, figs. 2, 5. 1957; Cavaco in Humbert, Fl. Madagascar 80: 26, fig. VII:5-7. 1959. TYPE: Central Madagascar. Without precise locality (ca. 1890), *Baron* 2954 (lectotype, K, here designated; isoelectotype, P).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

Monoecious tree attaining 10 m tall and 30-40 cm D.B.H., the bark thin, gray, flaking, the new growth villous to velutinous with straight or matted simple hairs, the mature leafy stems 1.5-3 mm diam., dark brown, villous, glabrescent. Leaves opposite to subopposite, petiolate; petioles villous-hirsute, 4-12 mm by 1-1.2 mm; lamina chartaceous to subcoriaceous, sparsely pilose abaxially, more densely so along the costa and major veins, adaxially glabrescent, ovate, elliptic to narrowly elliptic, oblong or narrowly oblong, lorate or rarely obovate, 40-115(-135) mm by 17-44 mm, the apex shortly acuminate, shortly acute, obtuse or emarginate, the base acute to obtuse, sometimes slightly decurrent, the secondary veins 4-9 pairs, making a 55-80° angle with the costa, the venation visible to 2(-3°) adaxially, to 3(-4°) abaxially, the margin thickened, slightly revolute. Inflorescence terminal, axillary or ramiflorous, cinereous, velutinous-tomentose, a unisexual or sexually mixed pleiochasium of 3-7(-9) flowers, usually terminated by a single gynoeceous flower, the floral axis 5-30 mm by 1.2-2 mm, the axis and pedicels sub-

tended by naviculate-subulate bracteoles 1-3.5 mm long. Androeceous flower in bud finely cinereous-tomentose, globose to globose-depressed, 6-7 mm diam. by 5-6 mm long, apiculate with 4 narrowly acute tepals ca. 1 mm long, the pedicel 8-10 mm by 0.6-1 mm; at anthesis deeply 4-fid, 15-18 mm diam., the lobes spreading flat; stamens ca. 75-90, deltoid to ovoid-ellipsoid, slightly recurved, 1.2-2 mm long by 0.8-1.2 mm wide, the loculi $\pm$ unilateral, introrse, separate, occupying $\frac{2}{3}$ - $\frac{3}{4}$ total length of the stamen, the filament subsessile, the internal receptacle surface with scattered to dense simple hairs between the stamens. Gynoeceous flower in bud subglobose-napiform, more densely tomentose than androeceous flower, apiculate with 4 acutely deltoid tepals, the pedicel 10-15 mm by 1-1.2 mm; at anthesis 7-9 mm diam. by 5-6 mm long, the orifice X-shaped, 3-3.5 mm diam., splitting into 4 deltoid, suberect to outcurved lobes; styles numerous, ca. 150-200, narrowly conical, 1-1.5 mm long by 0.4-0.6 mm wide basally, the surface strongly papillose, the internal receptacle surface densely velutinous-tomentose between the styles. Fruiting receptacle usually solitary on leafless stems, $\pm$ shallowly cupuliform, 30-50 mm diam. by 20-35 mm long, the cavity shallow to almost absent, the external surface pale, mottled corky brown, the orifice comprising $\frac{1}{3}$ - $\frac{1}{2}$ total width of the fruit, subentire, the walls 15-25 mm thick, the internal surface with scattered, narrowly conical papillose styles 0.5-0.7 mm long by 0.5 mm wide basally, interspersed with scattered to dense hairs; pedicel and peduncle tapered, to 55 mm long by 4-5 mm diam. medially. Mature carpels 7-8 mm long, 4-5 mm wide, 3-4 mm thick, ovoid-compressed, the endocarp light brown, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 27).

Habitat. *Tambourissa hildebrandtii* displays a wide ecological amplitude comparable to that of *T. purpurea*. It ranges from the *Tambourissa/Weinmannia* montane wet forest zone above 800 m in the eastern region, to montane forests of the central plateau (ca. 1,000-1,400 m) and extends to the dry semideciduous forests of the western domain where it finally disappears.

MADAGASCAR. FIANARANTSOA: Fianarantsoa (fr), *Anon. sub* SF 2145 (MAD); Inselbergs W of Ambalavao, at Pk 475, 970 m, 31 Jan. 1975 (fl, fr), *Croat* 30194 (MAD, MO); National Route no. 7 at 11 km

W of Ambalavao, 950 m, 5 Nov. 1978 (fl, fr), *Lorence 2043* (MAD, MAU, MO). MAJUNGA: Natural reserve no. 8, Namoraka (Saolala), 7 Feb. 1951 (fr), *Anon. sub RN 3298* (MAD). TAMATAVE: Ambatondrazaka (near Lake Alaotra) (fl, fr), *Anon. sub SF 1723* (MAD); Ambohijanahary, 1,000 m (by Lake Alaotra), 5 Jan. 1945 (fl), *Anon. sub SF 2188* (MAD); small forest at Marovato, East Manaka (near Lake Alaotra), 13 Nov. 1946 (fl), *Anon. sub Herb. Alaotra 3102* (MAD, 2 sheets); Didy Forest, Ambatondrazaka (near Lake Alaotra), ca. 1,200 m, 5 July 1952 (st), *Anon. sub SF 5498* (MAD); 2 June 1952 (fl), *Botoalma sub SF 4145* (MAD, 2 sheets); Andevorante, Moramanga, 5 Oct. 1912 (fl), *Afzelius s.n.* (K). TANANARIVE: Finoarive, 1,400–1,600 m, 18 Mar. 1930 (fl, fr), *Decary 7633* (K, 2 sheets); Bongolave, 800–900 m, Tsiroanandidy, July 1974 (fr), *Morat 4608* (MAD). TULEAR: upper basin of the Mandrare River (SE), pass and summit of Marosoui, 1,000–1,400 m, 14–15 Nov. 1928 (fr), *Humbert 6606* (B). PROVINCE UNCERTAIN: Arkotreano, forest N of the road to Nickelville, 29 Dec. 1944 (fl, fr), *Anon. sub Herb. Alaotra 2091* (MAD, 2 sheets); Menavavakely, Mevatanana, 16 Apr. 1951 (fl), *Anon. sub SF 3588* (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, Jan. 1882 (fr), *Baron 1144* (K, P, syntypes of *T. baroni*); (fl), *Baron 2417* (K, P); 1883 (fl), *Baron 2477* (K).

Tambourissa hildebrandtii belongs to species Group 1B and is distinguishable from other members of the group, notably its closest ally, *T. nosybensis*, by its strongly papillose styles, fruiting receptacle with a very small to almost nonexistent central cavity, and its villous stems. The type of *T. baroni* has fewer flowers and smaller, more obtuse leaves than that of *T. hildebrandtii*, but easily falls within the range of variation displayed by the species. A comparable degree of variation in leaf size and shape frequently occurs on a single individual (e.g., *Lorence 2043*, MAD, MAU, MO).

Fresh flowers of *Tambourissa hildebrandtii* are externally grayish green to peach colored. The gynoecious flowers have purple styles, whereas the androecious flowers are beefy red within and produce a sweet, fruity odor. In mixed inflorescences, anthesis occurred in gynoecious flowers before it occurred in androecious flowers (*Lorence 2043*).

Vernacular names. Ambora, Ambora saha (Madagascar).

6. *Tambourissa nosybensis* Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 302, pl. 3, figs. 12, 13. 1982. TYPE: Madagascar. Diego Suarez: Nosy Be Island (Nossi-Bé); Lokobe, Natural Reserve no. 6, 350 m, 12 Dec. 1967 (fl), *Bernardi 11847* (holotype, G; isotypes, K, P, Z).

Monoecious to subdioecious tree 6 m tall, the bark pale gray, licheniferous, longitudinally fissured, the new growth pilose with short, fulvous hairs, the mature leafy stems terete, 2–3.5 mm diam., brown, pilosulous. Leaves opposite, petiolate; petioles 6–11 mm by 1–1.2 mm, pilose-pubescent; mature lamina adaxially glabrescent, abaxially sparsely hirsutulous, especially along the costa and major veins, brown, discolorous, subcoriaceous, narrowly elliptic to narrowly oblong, occasionally $\pm$ falcate, 60–125 mm by 20–36 mm, the apex acuminate, the base acutely cuneate, the secondary veins 4–6 pairs, making a 35–45° angle with the costa, the intersecondary and tertiary branches straight with strong ad-medial orientation, $\pm$ perpendicular to the costa, the venation visible to 2(–3°) adaxially, and to 3(–4°) abaxially, the margin slightly revolute, thickened. Inflorescence cauliflorous, moderately to densely fulvous velutinous, a unisexual or rarely sexually mixed pleiochasium of 9–12 flowers, the floral axis 50–87 mm by 2 mm, the pedicel and peduncle 7–20 mm by 1–2 mm, the joint swollen, subtended by a caducous, subulate-naviculate bracteole 1–2 mm long. Androecious flower in bud unknown; at anthesis deeply 5-fid, 17 mm diam., the lobes thick, spreading flat, the receptacle externally hirsute; stamens ca. 70, incurved, ovoid-acuminate, subsessile, 1.5–2 mm long by 0.7–1 mm wide, the loculi lateral, separate, the connective acute, prolonged for ca. 0.5 mm, the internal receptacle surface with rare, scattered hairs among the stamens; pedicel ca. 2 mm diam. Gynoecious flower in bud discoid-patelliform, 9–10 mm diam. by 3–4 mm long, longitudinally multi-ribbed, velutinous, the apex depressed, with 4 subulate tepals ca. 1 mm long, the pedicel 9–20 mm by 1–1.2 mm; at anthesis splitting apically into 4(–6) short, straight or incurved deltoid lobes, the orifice small, X-shaped; styles numerous, ca. 400, broadly conical to columnar, apiculate, 0.4–0.6 mm long by 0.4–0.5 mm diam. basally, not papillose, the internal receptacle surface velutinous between the styles. Fruiting receptacle unknown. Figure 28.

Distribution. Known only from Nosy Be Island off the northwestern coast of Madagascar (Fig. 29).

Habitat. *Tambourissa nosybensis* was collected in depauperate lower montane wet forest (presumably of Chlaenaceae, Myristicaceae, and *Anthostema*) at 350 m.



FIGURE 28. *Tambourissa nosybensis* Lorence.—A. Habit.—B. Androecious flower at anthesis.—C. Stamen, abaxial view.—D. Gynoecious inflorescence at anthesis.—E. Gynoecious flower at anthesis, apical view.—F. Gynoecious flower at anthesis, longitudinal section.—G. Styles, longitudinal section. All *Bernardi 11847* (G). Bars equal 10 mm in A, B, D, E, and 1 mm in C, F, G.



FIGURE 29. Distribution map of some *Tambourissa* species in Madagascar.

MADAGASCAR. WITHOUT PRECISE LOCALITY: ca. 1883 (fl), *Humbolt* 642 (K, P).

Tambourissa nosybensis belongs to species Group 1B. Although most closely allied to *T. hildebrandtii* (for which Bernardi mistook it), *T. nosybensis* possesses sufficient distinguishing characters to merit specific status (Table 15). These include a number of specialized features, notably the production of a mucilaginous exudate in the mature gynoeceous flowers (conspicuous in rehydrated flowers), and also an apparent trend towards dioecy. I first thought the species was dioecious but then found a single androeceous flower among some 34 gynoeceous flowers, suggesting it is monoecious. Further collections, particularly of androeceous flowers and fruit, and observations on the biology of this interesting species are required.

7. *Tambourissa decaryana* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957; Cavaco in Humbert, Fl. Madagascar 80: 22, fig. VI:1–4. 1959. TYPE: Madagascar. Tamatave: Mt. Vatovavy (Mananjary), 22 Nov. 1938 (fl, fr), *Decary* 13697 (holotype, P).

Cauliflorous tree 10–16 m tall, possibly dioecious (?), the new growth pilose-strigillose, the adult leafy stems terete, pilose, 4–5 mm diam. Leaves opposite, petiolate; petioles 15–20 mm by 2–4 mm, pilose; lamina subcoriaceous, oblong, 150–325 mm by 85–115 mm, adaxially glabrous, abaxially strigillose with white, appressed hairs, the apex acuminate, the base obtuse to rounded, the secondary veins 6–14 pairs, making a 60–70° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin slightly revolute. Androeceous flowers unknown. Gynoeceous inflorescence cauliflorous, a fulvous, tomentose or velutinous pleiochasium of 6–11 flowers, the floral axis (10–)30–135 mm by 1.5–3 mm, subtended basally by several deltoid-naviculate bracteoles ca. 1 mm long, the pedicel 6–23 mm by 1–1.5 mm, subtended by a velutinous subulate bracteole (1–)4–5 mm long. Gynoeceous flowers in bud napiiform-depressed, 7–8 mm diam. by 4–5 mm long, externally tomentose to velutinous, the apex apiculate with 4–5 minute velutinous tepals; at anthesis 8–11 mm diam. by 7–8 mm long, the orifice shallowly 4–5-fid, comprising $\frac{1}{2}$ – $\frac{3}{4}$ total width of the receptacle, the lobes suberect, the margins thickened; styles numerous, ca. 200–300, shortly conical, 0.4–0.5 mm long by 0.2–0.3 mm wide, basally $\pm$ ventricose, the apex acute, slightly papillose, the ovule amphitropous; receptacle lobes bearing internally several series of larger, sterile, hirsutulous conical appendages (ca. 25–40), these 1–1.5 mm long by 0.5–0.8 mm diam., the internal receptacle surface densely velutinous between the styles and on the lobes. Fruiting receptacle produced on the trunk and branches, cupuliform, 40–50 mm long by 50–70 mm diam., externally corky, the orifice comprising $\frac{1}{5}$ – $\frac{1}{3}$ total width of fruit, the styles conical, 0.5 mm long, interspersed with hairs; pedicel and peduncle 37–110 mm by 6–9 mm.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. *Tambourissa decaryana* occurs in the lower altitude Myristicaceae/*Anthostema* wet forest zone in the eastern domain, from ca. 250 to 500 m.

TABLE 15. Some distinguishing morphological features of *Tambourissa hildebrandtii* and *T. nosybensis*.

Character	<i>T. hildebrandtii</i>	<i>T. nosybensis</i>
Angle of secondary veins to costa	55–80°	35–45°
Intersecondary veins and tertiary branches	zig-zag, weak admedial orientation	straight, strong admedial orientation
Inflorescence position	ramiflorous or axillary	cauliflorous
Inflorescence pubescence	cinereous, hirsute, or tomentose	fulvous, velutinous
Stamens	outcurved	incurved
Loculi	unilateral	bilateral
Connective	short, obtuse, or absent	acute, 0.5 mm long
Gynoecious receptacle	subglobose-napiform, not longitudinally ribbed	discoid-patelliform, longitudinally ribbed
Orifice lobes	4, suberect to everted	4(–6), incurved or straight
Styles	narrowly conical, 1–1.5 mm long, strongly papillose	broadly conical to columnar, apiculate, 0.4–0.6 mm long, not papillose
Ovule	anatropous, pendulous	amphitropous, oblique
Mucilaginous exudate	absent	present, covering styles
Tanniferous cells	present	absent
Stone cells	absent	present

MADAGASCAR. TAMATAVE: Mt. Vatovavy, Mananjary Bassin, 250 m, Aug. 1911 (fr), *Perrier de la Bâthie* 10091 (P); Marolambo District, Andonabe Canton, near Ambatomitsangana, 16 Sept. 1963 (fr), *Anon. in SF-21357* (P); Ambodiriana (R.N. 1), 250–500 m, 21 Aug. 1957 (fr), *Capuron 18111-SF* (P). WITHOUT PRECISE LOCALITY: Feb. 1881 (fl), *Parker s.n.* (K).

Parker s.n. differs from the type of *Tambourissa decaryana* in having a longer, less densely pubescent floral axis, and furthermore has mature gynoecious flowers (*Decary 13697* is mostly in bud). Although *Parker s.n.* lacks leaves, the presence of large sterile appendages within the flowers, an abundance of oil cells in the receptacular ground tissue, amphitropous ovules, and production of mucilage by the styles all correspond well with the type of *T. decaryana*.

The species is characterized by a moderately to densely pubescent inflorescence, long bracteoles, 4–5-fid gynoecious flowers with an X-shaped orifice and suberect lobes, and sparsely pubescent leaves, characters which place it in species Group 1B. Its huge, macrophyllous leaves (assuming they are not from a vigorous sucker shoot) and presence of several rows of large, style-like sterile appendages surrounding the styles set it apart from all other Madagascan species, although *Tambourissa parvifolia* has similar appendages. The sterile appendages in *T. decaryana* resemble the styles but are 2–4 times larger, hirsutulous, and lack an ovule at the base. Numerous oil cells occur in the receptacular ground tissue. The species also displays certain special-

ized features shared with *T. nosybensis*, i.e., production of a mucilaginous exudate and a tendency towards dioecy.

8. ***Tambourissa humbertii*** Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 28, fig. IX:1–4 (non fig. VIII). 1959. TYPE: Madagascar. Fianarantsoa: high valley of the Rienana River, Matitanana Basin, 18–24 Nov. 1924 (fl), *Humbert 3593* (holotype, P; isotype P).

Large tree, the new growth velutinous, the mature leafy stems flattened, stramineate, 3.5–6 mm diam., sparsely hirsutulous, glabrescent. Leaves opposite, petiolate; petioles hirsutulous, glabrescent, 10–13 mm by 1.5–2 mm; lamina glabrous, subcoriaceous, elliptic to oblong, 82–126 mm by 35–60 mm, the apex shortly acute, the base acute, slightly decurrent, the secondary veins 6–9 pairs, making a 60–70° angle with the costa, the venation visible to 3° on both surfaces, the margin revolute, the adaxial laminar surface moderately lustrous. Dioecious? Androecious flowers unknown. Gynoecious inflorescence presumably cauliflorous, a fascicle of 2–3 flowers, or a short, 5–17-flowered pleiochasium, the floral axis stout, 30–50 mm long, lenticellar, canescent, the pedicel velutinous-canescant, jointed below the middle, the pedicel and peduncle 12–20 mm by 2–3 mm, with 1 to several velutinous, deltoid-naviculate basal bracteoles 1–2 mm long. Gynoecious flower in bud canescent, broadly

napiform-depressed, 13–15 mm diam. by 5 mm long, apiculate with several minute, coalescent velutinous tepals; at anthesis broadly napiform-discoid to patelliform, 18–21 mm diam. by 6–8 mm long, the orifice X-shaped, ca. 10 mm diam., splitting for ca. $\frac{1}{2}$ the length of the receptacle into 4(–5) suberect, fleshy deltoid lobes, the margins thickened; styles numerous, ca. 500 or more, densely crowded, ovoid-ventricose, 1–1.2 mm long by 0.5–0.7 mm wide basally, the apex shortly acuminate or apiculate, papillose, the surface bearing scattered simple hairs ca. 1–1.5 mm long, the internal receptacle surface velutinous between the styles and on the lobes the numerous short hairs mixed with scattered long hairs. Fruit unknown.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. *Tambourissa humbertii* is known only from the type collection, presumably from the *Tambourissa/Weinmannia* montane wet forest zone from ca. 1,000 to 1,400 m. Further collections of this striking species, particularly androecious flowers and fruit, and observations on its life history are needed.

In contrast to Cavaco's (1957b) statement that *Tambourissa humbertii* approaches *T. ficus* from Mauritius, I find that it differs from the latter species in several important characters. Most notably it lacks the ternate-whorled to subalternate leaves and tanniferous idioblasts in the floral ground tissue characteristic of *T. ficus*. *Tambourissa humbertii* appears rather to belong to species Group 1B and is distinguishable from other members of the group by its much larger gynoecious flowers and presence of long hairs on the styles. Styles of *T. kirkii* (Group 2B; Comores), incidentally, bear similar but shorter scattered hairs. In addition, the internal surface of the gynoecious receptacle of *T. humbertii* bears mixed long and short hairs, a feature found in no other species.

In spite of their relatively large size, gynoecious flowers of *Tambourissa humbertii* structurally most closely resemble those of *T. decaryana*. In both species the orifice lobe margins are conspicuously thickened and numerous oil cells occur in the ground tissue. Flowers of *T. humbertii* are much larger, however, and lack the peculiar sterile appendages characteristic of the latter species.

9. *Tambourissa floricosata* Cavaco, Bull. Soc.

Bot. France 105: 39. 1958; Cavaco in Humbert, Fl. Madagascar 80: 40, fig. IV:7–11. 1959. TYPE: Madagascar. Tamatave: Analamazaotra forest, Feb. 1919 (fl), *Ramantoavolana sub T. Thouvenot* 134 (holotype, P; isotypes, P, 2 sheets).

Schrameckia madagascariensis Danguy, Bull. Mus. Hist. Nat. (Paris), Ser. 1, 28: 249. 1922 non *Tambourissa madagascariensis* Cavaco, 1957.

Monoecious tree 18–20 m tall, the new growth unknown, the mature growth subglabrous, the mature leafy stems terete, 1.5–2 mm diam. Leaves opposite to subopposite, petiolate; petioles 7–13 mm by 0.8–1 mm; lamina subcoriaceous to coriaceous, glabrous, elliptic to obovate, rarely oblong, occasionally slightly falcate basally, 35–85 mm by 15–36 mm, the apex obtuse to retuse, its extremity usually thickened or apiculate, the base acutely cuneate to acutely decurrent, the secondary veins 4–7 pairs, making a 55–60° angle with the costa, the venation visible to 3° adaxially and to 4° abaxially, the margin thickened, slightly revolute. Inflorescence ramiflorous, a puberulent, sexually mixed pleiochasium of (3–)5–9 flowers attaining 120–160 mm by 60–70 mm, axillary or on leafless nodes, or the flowers solitary and axillary or terminal, the floral axis (17–)23–140 mm by 1–3 mm, $\pm$ flattened, often leafy. Androecious flower in bud quadrangular-globose, 9–12 mm diam., with 2–4 prominent longitudinal ridges, apiculate with 4 deltoid-rounded hirsute tepals; pedicels 16–30 mm by 1–1.5 mm, flattened, puberulent, each subtended by a naviculate-deltoid bracteole; at anthesis 4-fid, 25 mm diam., splitting to ca. $\frac{1}{2}$ – $\frac{2}{3}$ total length of the receptacle, the lobes incurved, not spreading, each lobe with ca. 2 fleshy, obtuse scale-like tepals internally near the apex; stamens 16–22, large, ovoid to deltoid, acute, 3–4.5 mm long by 1.5–2.5 mm wide, the loculi lateral, free, the connective broad, $\pm$ sessile, the apex apiculate, acute, the internal receptacle surface $\pm$ glabrous. Gynoecious flowers solitary and axillary or terminal on the mixed inflorescence, the receptacle globose-depressed, 13–18 mm diam. by 5–7 mm long in bud, with 2 lateral ridges, the orifice small, 1–2 mm diam., flanked by 4 obtuse, decussate tepals; pedicels to 55 mm by 2 mm. Immature fruiting receptacle ca. 47 mm diam., broadly napiform-depressed, the orifice ca. 5 mm diam., subentire, the external surface corky brown, the internal surface with numerous scattered, shortly conical styles ca. 0.5–1 mm long by 0.5 mm wide

basally, the surface between the styles hirsute. Submature fruiting receptacle solitary on leafless stems, shallowly cupuliform, 20 mm long by 45–57 mm diam., externally venose, corky, the pedicel and peduncle tapered, 120–150 mm by 4–5 mm; mature carpels unknown.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. Known only from three collections, all from the Perinet area (Analamazaotra), in the *Tambourissa/Weinmannia* wet forest zone from ca. 900 to 950 m. *Thouvenot 134* was collected in February with flowers and young fruit. As the Analamazaotra forest is included in a nature reserve, it is probable that *T. floricosata* still occurs there; much intact forest still remained in 1978. However, additional flowering and fruiting collections and data on its life history are needed.

MADAGASCAR. TAMATAVE: Analamazaotra, Feb. 1912 (seed), *Perrier de la Bâthie 10128* (P); Zedsiadra (or Djedsiatsa?) near Perinet (st), *Schedl 40* (MAD).

In spite of the large size and small number of stamens in androecious flowers of *Tambourissa floricosata*, the species possesses a number of attributes which suggest inclusion in species Group 1C, along with *T. parvifolia* (Table 5). It differs from the latter species by its larger leaves, flowers, and receptacles with two to four prominent external longitudinal ridges.

Vernacular names. Ambora, Ambora lahy, Ambora vavy (Madagascar).

10. *Tambourissa parvifolia* Baker, J. Bot. n.s. 11: 267. 1882; Baillon, Bull. Mens. Soc. Linn. Paris 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 36, fig. X:1–4. 1959. TYPE: Madagascar. Without precise locality ("Central Madagascar," probably Tananarive): 1880 (fl), *Parker s.n.* (holotype, K).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

Monoecious treelet or tree 5–15 m tall, the new growth sparsely hirsutulous, glabrescent, the mature leafy stems 1.5–3.5 mm diam. Leaves opposite, petiolate; petioles 3–5 mm by 0.7–1 mm; lamina glabrous, coriaceous, elliptic to oblong or obovate, 15–47 mm by 9–22 mm, the apex obtuse to retuse, the base acutely cuneate to obtuse, slightly decurrent, the secondary veins 4–5 pairs,

making a 55–60° angle with the costa, the venation obscure adaxially or the 2° veins scarcely visible, abaxially visible to 3°, the margin revolute. Inflorescence ramiflorous on leafless stems, an (always?) unisexual, hirtellous-puberulent pleiochasium of 2–11 flowers, the floral axis 12–70 mm by 1–2 mm, basally bracteolate. Androecious flower in bud globose, 5–6 mm diam., apiculate with several minute, coalescent tepals, the pedicel 6–10 mm by 1–2 mm, subtended by a deltoid, hirsute bracteole 2 mm long by 1 mm wide; at anthesis deeply 4-fid, 17–30 mm diam., the lobes spreading flat, the internal receptacle surface bearing several sterile, columnar appendages near the apex of the lobes; stamens ca. 50–60, ± ligulate, 1–1.5 mm long by 0.6–0.8 mm wide, the loculi lateral, free, parallel, comprising ca. ¾ total length of the stamen, the connective not or only slightly prolonged, the internal receptacle surface glabrous. Gynoecious receptacle at anthesis subglobose to napiform, ca. 9–10 mm diam., externally hirsutulous-pubescent, the orifice small, 4-lobed, X-shaped, comprising ca. ¼ total width of the receptacle, the pedicel 7–14 mm long; styles numerous, ca. 200 or more, conical, ca. 0.5 mm long by 0.5 mm wide basally. Fruiting receptacle solitary or in pleiochasia of 2 or more, the axis to 60 mm by 5 mm, hirtellous, the receptacle shallowly cupuliform to napiform-depressed, 30–95 mm wide by 25–40 mm long, the orifice comprising ca. ¼–½ total width of the receptacle, 8–12 mm wide, subentire with several thick, irregularly deltoid lobes, these bearing a number of sterile, clavate appendages 1–2 mm long on their internal surface, the external receptacle surface irregularly reddish brown with pale corky patches, glabrous or sparsely hirsutulous, the internal surface with numerous conical styles 0.3–0.5 mm long and wide basally with scattered simple hairs in between, the pedicel 10–22 mm by 3.5–6 mm. Carpels 5–13 mm long by 5–9 mm wide by 3–4 mm thick, ovoid-compressed, the endocarp tan, the surface scrobiculate.

Distribution. Endemic to Madagascar (Fig. 29).

Habitat. *Tambourissa parvifolia* is restricted to the sclerophyllous montane forest zone of the central plateau at elevations from ca. 1,400 to 2,000 m.

MADAGASCAR. ANTANANARIVO: E of Antsirabe, 2,000 m, 3–4 Nov. 1928 (fl), *Humbert 6351bis* (P); E slope of Ankaratra, 24–26 Mar. 1958 (fl), *Capuron 18507-*

SF (P). FIANARANTSOA: Andringitra, Imaisoa, 1,500–2,000 m, 28 Oct. 1960 (fl), *Leandri et al.* 3393 (P). WITHOUT PRECISE LOCALITY: Central Madagascar, 1855 (fr), *Baron* 3864 (BM, K, P); (st), *Baron* 4204 (P); (fr), *Baron* 4205 (K); (fr), *Baron* 6048 (P); (fl), *Parker s.n.* (P, 5 sheets).

The sclerophyllous leaves of *Tambourissa parvifolia* are smallest of any known species of *Tambourissa* and probably represent an adaptation to the high altitude montane habitat. In fact, sclerophylly characterizes the majority of arborescent species occurring in this habitat in Madagascar, which has been termed the “forêt dense sclerophylle de montagne” (Koechlin et al., 1974).

In spite of its extremely reduced leaves, *Tambourissa parvifolia* is best placed in species Group 1C along with *T. floricosata*. It displays a number of specialized trends, including reduced leaves, a tendency towards unisexual inflorescences (and possibly dioecy) and the presence of sterile, style-like appendages on the internal surfaces of the receptacle lobes, a feature shared with *T. decaryana*. *Tambourissa parvifolia* is easily distinguished from *T. floricosata* by its small, obtuse or emarginate leaves and slender anther filaments.

Vernacular names. Ambora, Amboravato (Madagascar).

- 11. *Tambourissa beanjadensis*** Lorence, nom. nov. *Ehippiandra capuronii* Cavaco, Bull. Soc. Bot. France 104: 610. 1957; Cavaco in Humbert, Fl. Madagascar 80: 8, fig. I:10–12. 1959 non *Tambourissa capuronii* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957. TYPE: Madagascar. Diego Suarez: Beanjada Massif (N of the Masoala Peninsula), E forest at its upper limits (“forêt des cimes”), ca. 1,100 m, 30 Dec. 1953 (fl), *Capuron* 8826 bis-SF (holotype, P).

Medium-sized monoecious tree, the new growth with rare, scattered hairs, the mature leafy stems glabrous, brown, 1.5–2 mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles 6–9 mm by 1 mm; lamina chartaceous to subcoriaceous, adaxially lustrous, minutely punctate, elliptic, (23–)34–47 mm by (12–)18–28 mm, the apex abruptly and shortly acuminate, the tip thickened, the base cuneate to broadly cuneate, rarely obtuse, the secondary veins 3–5 pairs, making a 75–85° angle with the costa, adaxially scarcely visible, abaxially prominent,

the venation visible to 3° abaxially, the margin entire, slightly revolute. Inflorescence ramiflorous or cauliflorous, solitary or clustered, an apparently unisexual pleiochasium of 3–7 flowers, or the flowers rarely solitary, the floral axis 20–40 mm by 1 mm, pilose when young, glabrescent, subtended by several minute, naviculate bracteoles 1 mm long, the pedicel 3–7 mm by 1 mm, subtended by a minute, obtuse naviculate bracteole ca. 1 mm long. Androecious flower in bud globose, 4 mm diam., glabrous, the apex with 4 sparsely pilose obtuse tepals; at anthesis deeply (3–)4(–5)-fid, 8–10 mm diam., the lobes spreading flat, each bearing internally near the apex a small, scale-like tepal 1 mm wide; stamens ca. 35–36, obtuse to deltoid, 0.6–1 mm long and wide, the filament short or sessile, the loculi confluent apically into a single, crescentiform locus occupying $\frac{2}{3}$ or more of the total length of the stamen, the connective thick, not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud globose-napiform, ca. 6 mm diam. by 4–5 mm long, glabrous, the apex with 4 minutely puberulent obtuse tepals; at anthesis splitting into an X-shaped orifice ca. 1–2 mm wide, the 4 lobes deltoid, the internal receptacle surface with a pubescent ring near the orifice; styles numerous, ca. 200, shortly and broadly conical, 0.3–0.4 mm long and wide, papillose, producing a mucilaginous exudate, the internal receptacle surface with scattered hairs between the styles, the receptacle wall 1 mm thick. Fruiting receptacle unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. The species is known only from the type collection from the upper limits of what is presumably mid altitude *Tambourissa*/*Weinmannia* wet forest on mountainous summits. Further collections and field observations are obviously needed.

Features which immediately place this species in the genus *Tambourissa* are the closed, globose gynoecious floral receptacle with an X-shaped orifice and the conical carpels completely immersed in and fused with the receptacle wall. The broadly deltoid, sessile stamens with a single, crescentiform locus and presence of tepals on the inner surface of the androecious receptacle lobes occur in a number of other *Tambourissa* species, as previously noted. Pollen of the species, figured by Walker (1976) and presumably taken

from the type, also conforms to that of *Tambourissa* rather than that of *Ehippiandra*.

The small leaves and ramiflorous to cauliflorous, pleiochasial inflorescence of *Tambourissa beanjadensis* resemble those of *T. parvifolia*, which differs by its more coriaceous, obtuse leaves, much larger androecious flowers, and longer stamens with distinct filaments and separate loculi. *Tambourissa beanjadensis* is probably best placed in species Group 2A, however, a diverse series of species from Madagascar, Réunion, and the Comores characterized by their deeply 4-fid androecious flowers which spread flat open and have stamens with unprolonged connectives. Its gynoeceous flowers, like those of the two Réunion species in this subgroup (*T. crassa* and *T. elliptica*) are globose-depressed, open by an X-shaped orifice, are nearly glabrous within, and produce a mucilaginous exudate. Both latter species are easily distinguished by their much larger leaves, obtusely columnar styles, and stamens with separate thecae.

12. *Tambourissa madagascariensis* Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 30, fig. IX:5–8. 1959. TYPE: Madagascar. Majunga: Natural Reserve no. 4 (Tsaratanana, Ambanja), Mangindrano Canton, Bealanana District, 7 July 1953 (fl), *Rababoto sub R.N. 6028* (holotype, P).

Dioecious (?) tree 5–15 m tall, or a lianescent shrub, the new growth with scattered hairs, glabrescent, the mature leafy stems glabrous, 2–3 mm diam., with longitudinal striations. Leaves glabrous, opposite to subopposite, petiolate; petioles 4–7 mm by 1–1.5 mm; lamina chartaceous, broadly elliptic, 42–80 mm by 24–34 mm, the apex acuminate, the tip $\pm$ indurated, the base acutely or rarely obtusely decurrent, the secondary veins 5–7 pairs, making a 60–70° angle with the costa, the venation obscure, visible to 2° adaxially and to 3° abaxially, the margin plane to slightly revolute. Inflorescence ramiflorous, axillary or on leafless nodes, a subglabrous unisexual pleiochasium of 3–9 flowers, sometimes leafy in the terminal portion, the floral axis 20–85 mm by 1–2 mm, longitudinally striate, sparsely puberulent around the pedicels, subtended by several broadly deltoid, ciliate bracteoles. Androecious flower in bud globose, 6–7 mm diam., $\pm$ glabrous, apiculate, the tepals fused, the pedicel 8–23 mm by 0.6–1 mm, glabrous or sparsely

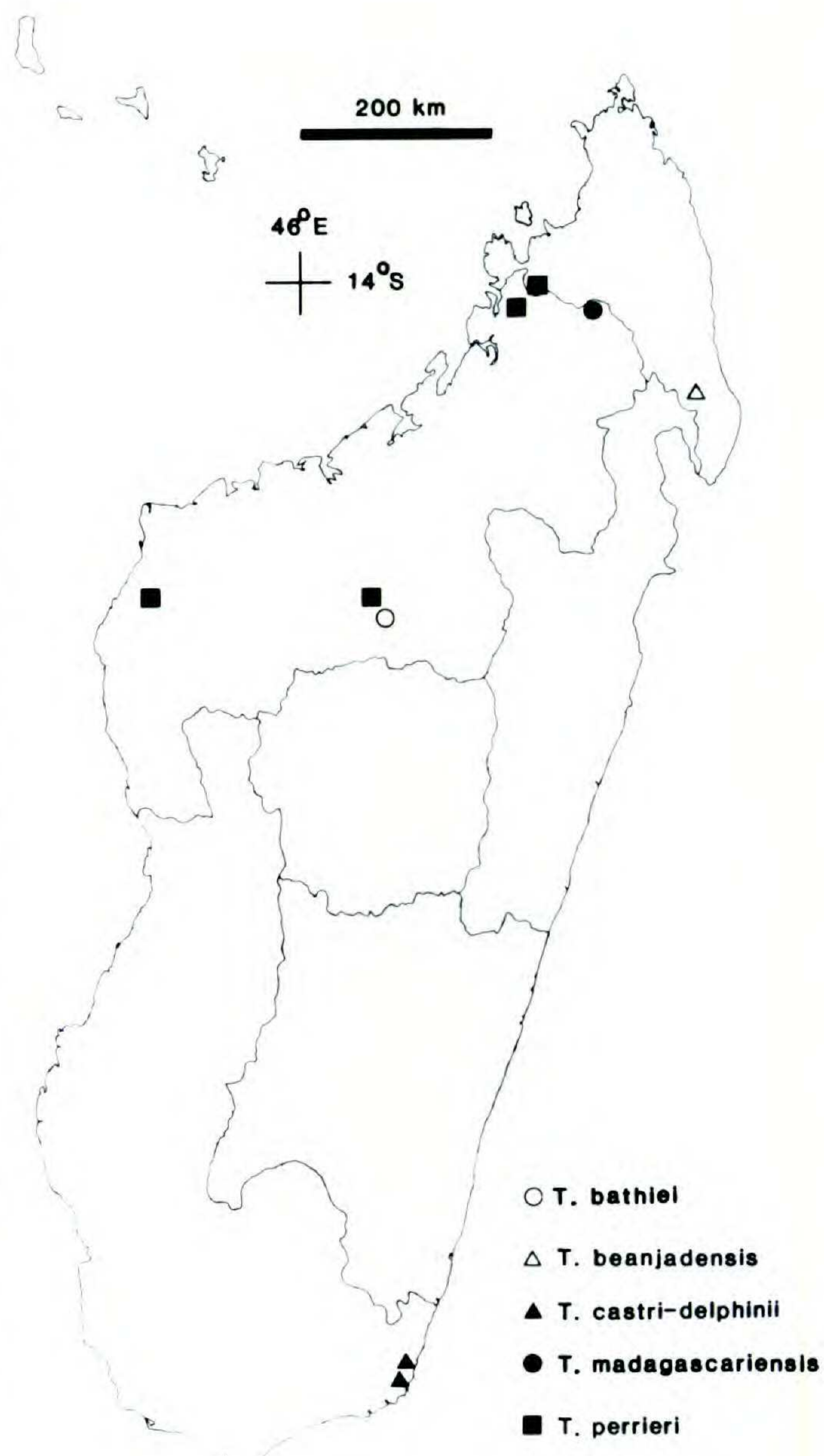


FIGURE 30. Distribution map of some *Tambourissa* species in Madagascar.

puberulent basally, subtended by a deltoid-subulate, ciliate bracteole 0.5–2.5 mm long; at anthesis deeply 4-fid, 20 mm diam., the lobes spreading flat; stamens numerous, ca. 200, lanceolate to subulate, 2.5–4 mm long by 0.7–1 mm wide, sessile or with a short filament, the loculi lateral, separate, occupying almost the entire length of the stamen, the connective slightly prolonged, obtusely apiculate, the internal receptacle surface glabrous. Gynoeceous flower in bud subglobose, slightly depressed apically, 4–5 mm diam., externally glabrous to sparsely hirsutulous; at anthesis (?) 5–6 mm diam., the orifice circular, entire, 2–3 mm diam., comprising ca. $\frac{1}{2}$ total width of the receptacle; styles numerous, several hundred, shortly columnar, 0.2–0.3 mm long, the apex rounded, the internal receptacle surface puberulent around the orifice and be-

tween the styles, the pedicel 6–8 mm long, shorter than in the androecious flower. Mature fruiting receptacle cupuliform, attaining 150 mm diam. (fide notes on *Anon. sub SF 2126*, MAD); carpels unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. The type of *Tambourissa madagascariensis* was collected on the Tsaratanana massif (northern Madagascar), presumably in montane wet forest of *Tambourissa/Weinmannia* above 1,000 m. The three other known collections of this species are from montane *Tambourissa/Weinmannia* wet forest (800–1,000 m), and Myristicaceae/*Anthostema* wet forest (ca. 400–800 m) in the eastern region. This seemingly disjunct distribution pattern may be the result of undercollecting.

MADAGASCAR. TAMATAVE: Mt. Ambatosoratra, 400 m, 4 Jan. 1949 (fl), *Anon. sub Herb. Alaotra 3247* (MAD); forest N of the road to Nickelville, on the banks of the Amkotreano River, 29 Dec. 1944 (fr), *Anon. sub Herb. Alaotra 2126* (MAD); wooded area on the summit of Mt. Analavorikely, 29 Dec. 1944 (fr), *Anon. sub Herb. Alaotra 2142* (MAD).

Tambourissa madagascariensis is anomalous in a number of respects and does not readily fit into any of the more or less natural groups of Madagascan species, but is best placed in species Group 2A. Its small, thin glabrous leaves are reminiscent of *T. purpurea* and *T. gracilis*, but the flowers are borne in long, slender subglabrous and long-pedicelled pleiochasia that are more suggestive of *T. gracilis*, *T. beanjadensis*, and *T. parvifolia*. Androecious flowers of *T. madagascariensis* are relatively large, however, and split open into four lobes which spread flat and bear numerous (ca. 200) long stamens with separate, parallel loculi, thus differing strikingly from the small, globular, nearly closed androecious flowers of *T. gracilis* and *T. purpurea*, which have short, sessile stamens with apically confluent loculi.

Gynoecious flowers of *Tambourissa madagascariensis* are small and globose-depressed with an entire, circular orifice that is internally puberulent, and numerous short, columnar-rounded styles suggestive of those species which produce copious mucilage at anthesis. The orifice apparently remains open throughout much of the floral development, thus differing markedly from the gynoecious flowers of *T. beanjadensis* and *T. parvifolia* (unknown in *T. gracilis*), which open

by an X-shaped orifice at anthesis and, furthermore have conical styles.

In terms of both androecious and gynoecious floral structure, *Tambourissa madagascariensis* appears to be most closely related to two of the Comorean species in Group 2A, *T. comorensis* and *T. leptophylla*, although their leaves and flowers are much larger. Presence of abundant oil cells in the gynoecious floral ground tissue of all three species and large fruits are common features. This group of Comorean species could have been derived from a common ancestor similar to *T. madagascariensis*.

Tambourissa madagascariensis also appears to share characters of androecious and gynoecious floral morphology with *T. elliptica* subsp. *micrantha* from Réunion, notably the pleiochasial inflorescence, similar androecious flowers and stamens, and gynoecious flowers with short, columnar styles and a mucilaginous exudate. Gynoecious flowers of the latter species lack the open, circular orifice, however.

Vernacular names. Ambora, Mahimasina, Valiramarnia (Madagascar).

13. *Tambourissa elliptica* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Cordem., Fl. Réunion 301. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. *Ambora elliptica* Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 304. 1855. TYPE: Réunion. Woods of the Hauts de la Rivière des Galets, July 1851 (fr), Boivin s.n. (holotype, P).

Tambourissa amplifolia sensu Cordem., Fl. Réunion 301. 1895 non (Boj. ex Tul.) A.DC.

Treelet or tree of variable habit, attaining 12 m tall, the new growth glabrous or with sparse, scattered hairs, the mature leafy stems terete, 2–6(–8) mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles (8–)10–25 mm by 1.5–5 mm; lamina chartaceous to coriaceous, narrowly to broadly elliptic, oblong, obovate-elliptic, obovate, broadly obovate or orbiculate, (50–)80–180(–250) mm by (15–)25–140(–190) mm, the apex shortly acuminate, acute, obtuse or rarely rounded, the base acutely decurrent, acutely cuneate to obtuse, truncate or subcordate, the secondary veins (5–)6–12 pairs, making a 55–75° angle with the costa, the venation prominent, raised, visible to 3–4(–5°) adaxially, to 4–5(–6°) abaxially, the margin plane to slightly revolute. Leaves of seedlings and suckers hetero-

phyllous, small and apically dentate in subsp. *elliptica*, long, narrow and entire in subsp. *micrantha*. Inflorescence subglabrous, a short ramiflorous pleiochasium (in subsp. *micrantha*), or the flowers solitary, sometimes axillary (in both subspecies), or cauliflorous and the flowers solitary or in fascicles of 2–3 (in subsp. *elliptica*). Androecious flower in bud globose, 7–15 mm diam., apiculate with 4 minute, obtuse tepals, the pedicel 10–40(–60) mm by 1–1.5 mm; at anthesis (3–)4(–5)-fid, 16–45 mm diam., the lobes spreading flat; stamens numerous, 65–300, ligulate to linear-ellipsoid, 1.5–6.5 mm long by 0.5–1 mm wide, the filament distinct, the loculi lateral, comprising $\frac{2}{3}$ – $\frac{3}{4}$ total length of the stamen, separate or confluent at the obtuse apex, the connective not prolonged, the internal receptacle surface glabrous. Gynoecious flower in bud globose-depressed to napiform-depressed, apiculate with several pairs of minute tepals, the pedicel (5–)10–20(–40) mm by 0.6–2 mm; at anthesis 6–15 mm diam., the orifice X-shaped, 1–5 mm wide, splitting into 4 shallowly deltoid lobes; styles numerous, ca. 150–200 or more, bluntly columnar, polyhedral, 0.5 mm long by 0.2–0.5 mm wide, the internal receptacle surface glabrous or with rare scattered hairs, producing a mucilaginous exudate. Fruiting receptacle solitary or in clusters of 2–3 on the trunk (subsp. *elliptica*), or on the leafless branches (subsp. *micrantha*), urceolate-globose or cupuliform, 25–90 mm diam. by 15–50 mm long, the orifice subentire, comprising ca. $\frac{1}{5}$ – $\frac{1}{2}$ total width of the fruit, the external surface pale corky brown or mottled with dark patches, the internal surface subglabrous with short scattered, columnar-polyhedral styles 0.5 mm wide. Mature carpels ovoid, 9–12 mm long, 5–7 mm wide, 3–4 mm thick, the endocarp whitish (subsp. *elliptica*) or pale brown (subsp. *micrantha*).

Distribution. Endemic to the wet and cloud forest zones of Réunion Island (Fig. 31).

E. J. de Cordemoy recognized four species of *Tambourissa* in his “Flore de l’Île de la Réunion” (1895), but used names of a Madagascan (*T. religiosa*) and a Mauritian (*T. quadrifida*) species for two endemic Réunion taxa that I have named *T. crassa* and *T. elliptica* subsp. *micrantha* respectively (Lorence, 1982).

Tambourissa elliptica, the only previously described species from Réunion, is quite polymorphic, but two modally distinct subspecies are distinguishable both by morphology, and, to a lesser

degree, altitudinal distribution. Both subspecies are monoecious with pink or pale yellowish white flower color morphs (never dark purple as is *T. crassa*), caulinary flowers, conspicuous higher order venation, contain stone cells in the floral ground tissue, and have a less well-developed hypodermis than in *T. crassa*, the second Réunion species.

Subspecies *elliptica* consists of a series of mostly mid to upper elevation forms which Cordemoy considered to represent two distinct species (*T. elliptica* and *T. amplifolia*, respectively), based on leaf characters which prove to be variable. Subspecies *micrantha* usually occurs at lower elevations, particularly in the southeastern part of the island where the most lowland wet forest still remains.

Each subspecies tends to occupy its own altitudinal zone throughout much of Réunion (Fig. 31), at least in higher altitude wet and cloud forest, significant portions of which are still preserved due to the island’s accentuated relief and steep, inaccessible slopes largely unsuitable for cultivation. A thorough distributional analysis is not possible for the lowlands, however, because little natural wet forest habitat remains there.

KEY TO THE SUBSPECIES OF *TAMBOURISSA ELLIPTICA*

- 1a. Flowers large, usually solitary or fasciculate, cauliflorous or ramiflorous; androecious buds 13–14 mm diam.; expanded androecious flowers 30–45 mm diam., the stamens ca. (100–)200–300 in number, (3–)4–6.5 mm long; gynoecious flowers 10–12 mm diam.; fruiting receptacle 45–90 mm diam.; sparse treelets or small, slender trees; medium to high elevations (1,000–2,000 m, rarely lower) 13a. subsp. *elliptica*
- 1b. Flowers smaller, usually in pleiochasia, sometimes solitary, always ramiflorous or axillary; androecious buds 8–10 mm diam.; expanded androecious flowers 20–25(–27) mm diam.; large trees with dense crowns; lower elevations, (200–600 m, rarely higher) 13b. subsp. *micrantha*

13a. *Tambourissa elliptica* subsp. *elliptica*.

Monoecious or subdioecious treelet or small tree attaining 6 m tall and 25 cm D.B.H., the bark soft, corky, pale brown, the new growth glabrous, rarely with a few scattered hairs, the mature leafy stems terete, 3–6(–8) mm diam. Leaves glabrous, opposite to subopposite, petiolate; petioles 10–25 mm by 2–5 mm; lamina subcoriaceous to coriaceous, elliptic to broadly

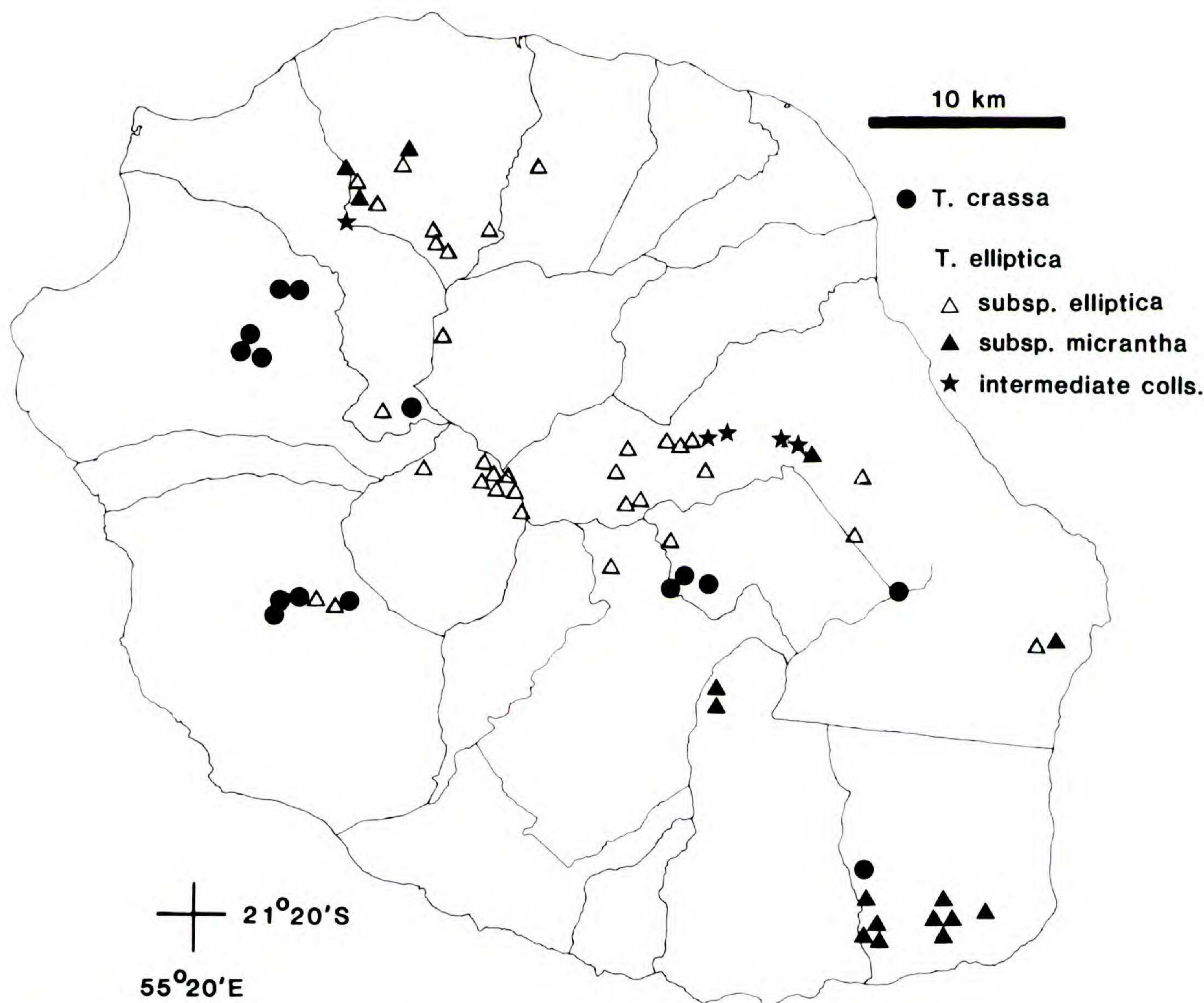


FIGURE 31. Distribution map of *Tambourissa* in Réunion.

elliptic, obovate to broadly obovate or orbiculate, 100–180(–250) mm by 60–140(–190) mm, the apex acute, rarely acuminate, obtuse or retuse, the base acute to obtuse, cuneate to decurrent, truncate or subcordate, the secondary veins 6–8 pairs, making a 55–75° angle with the costa, the venation prominent, visible to 3(–4°) adaxially and to 4(–5°) abaxially, the margin slightly revolute; juvenile and sucker leaves heterophyllous, with 1–2 pairs of glandular teeth in the apical portion of the lamina, the petiole red when living. Inflorescence glabrous or rarely with scattered hairs, the flowers solitary or in fascicles of 2–3 on meristematic swellings along the trunk, or the flowers ramiflorous and usually solitary, either axillary or on leafless nodes. Androecious flower in bud globose, (8–)12–15 mm diam., apiculate with several $\pm$ coalescent pairs of minute, glabrous tepals, the pedicel 20–40(–60) mm by 1–1.5 mm, jointed near the base with the short peduncle, subtended by several pairs of small,

deltoid, decussate ciliate bracteoles; at anthesis 4(–5)-fid, 30–45 mm diam., the lobes spreading flat; stamens numerous, (100–)200–300, ellipsoid to linear, 3–5 mm long by 0.6–1 mm wide, the filament broad, distinct, comprising ca. $\frac{1}{4}$ – $\frac{1}{3}$ total length of the stamen, the loculi subparallel, lateral, connivent or confluent at the obtuse apex, comprising $\frac{2}{3}$ – $\frac{3}{4}$ total length of the stamen, the connective not prolonged, the internal receptacle surface glabrous, glaucous. Gynoecious flower in bud globose-depressed to napiform-depressed, apiculate with several pairs of minute, $\pm$ coalescent tepals, the pedicel 5–10(–40) mm by 1.2–2 mm, jointed near the base with the short peduncle, subtended by several pairs of decussate bracteoles; at anthesis 8–15 mm diam. by 5–10 mm long, the orifice 4-fid, 2–5 mm diam., X-shaped with 4 short, straight to incurved deltoid lobes; styles numerous, ca. 200 or more, bluntly columnar, ca. 0.5 mm long by 0.2–0.5 mm wide, $\pm$ polyhedral, the internal receptacle

surface glabrous or with rare, scattered hairs. Fruiting receptacle solitary on the trunk or major branches, urceolate-globose, 45–90 mm diam. by 30–50 mm long, the orifice 10–30 mm diam., comprising $\frac{1}{5}$ – $\frac{1}{3}$ total width of the receptacle, subentire with remnants of the lobes, the external surface light corky brown, the internal surface glabrous, corky, with numerous short, $\pm$ polyhedral styles ca. 0.5–1 mm wide by 0.2–0.5 mm long, the apex flat or depressed, the pedicel and peduncle 10–60 mm long by 8–10 mm diam. Mature carpels ovoid-compressed, 10–12 mm long, 5–6 mm wide, 3–4 mm thick, the endocarp whitish, the surface smooth, unsculptured. Gametic chromosome number $n = 19$.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. It ranges from lower montane wet forest at altitudes from ca. 200 to 1,100 m, to cloud forest at altitudes from ca. 1,100 to 2,000 m.

RÉUNION. BÉBOUR: from Bébour to Casse de Tacamaca, 1,350–1,220 m, 18 Jan. 1975 (fl), *Bernardi 15151* (G, 2 sheets; P); Bébour Plateau, 8 Nov. 1972 (fr), *Bosser 21498* (P); on Piton Rond, ca. 1,800 m (fl), *Coode et al. 4223* (K, REU); Piton Rond, 1,300–1,600 m, 23 Feb. 1979 (fl), *Lorence 2431* (MAU, MO); (fl), *Lorence 2432* (MO); (fl, fr), *Lorence 2433* (MAU, MO). BOIS BLANC: Hauts de Bois Blanc, 600 m, July 1972 (fr), *Friedmann 1891* (P). BRAS JEANNE: Oct. 1944 (st), *Rivals s.n.* (TL-R); along canal of Bras Jeanne, Oct. 1944 (st), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: Hauts du Brûlé de St. Denis, Mar. 1943 (st), *Rivals s.n.* (TL-R); Ilet à Quinquina, near St. Denis, July 1945 (st), *Rivals s.n.* (TL-R). CIRQUE DE CILAOS: Mare à Joseph forest, 1,400 m, 25 Mar. 1967 (st), *Cadet 664 bis* (REU); 19 July 1975 (fl), *Cadet 4946* (REU); 22 Feb. 1975 (fl), *Cadet 5062* (REU); Petit Matarum, 1,700 m, 22 Feb. 1975 (fl), *Cadet 5055* (REU); R bank of Bras de Benjoin, road to Cilaos, 950 m, 3 Feb. 1968 (fl), *Capuron 28002-SF* (P, 2 sheets); Mare à Joseph above Cilaos, 1,400 m, 23 Feb. 1975 (fr), *Coode 4928* (K); (fl), *Coode 4929* (K); Coteau Kerveguen cloud forest, 1,500–1,700 m, 24 Feb. 1979 (st), *Lorence & Rolland 2437* (MAU, MO); (fl), *Lorence & Rolland 2438* (MO); (fl, fr), *Lorence & Rolland 2439* (MAU, MO); (fl), *Lorence & Rolland 2440* (MAU, MO); (fl), *Lorence & Rolland 2441* (MAU, MO); (fl, fr), *Lorence & Rolland 2442* (MAU, MO); Grand Matarum and Mare à Joseph, Aug. 1943 (st), *Rivals s.n.* (TL-R); Ilet des Salazes, Cilaos, 1,300 m, 21 Feb. 1944 (fl), *Rivals s.n.* (TL-R); slopes of the Piton des Neiges, 1,900–2,000 m (fr), *Rivals s.n.* (TL-R); Mare à Joseph, 1,200 m (fr), *Rivals s.n.* (TL-R). CIRQUE DE MAFATE: Mafate, Aug. 1883 (st), *Cordemoy s.n.* (TL-R); Sentier des Scouts, from Le Belier to top of Galets Gorge, ca. 1,800 m (fl), *Richardson 4136* (K). MOKA: Moka (st), *Rivals s.n.* (TL-R); 20 Feb. 1945 (fl), *Rivals s.n.* (TL-R); Hauts de Moka at the Chabries, 600 m, Apr. 1946 (fr), *Rivals s.n.* (TL-R). LA MONTAGNE: Grande Montagne, 1,200 m, 22 Mar. 1968 (fr), *Cadet 1291* (REU). NOUVELLE: La Nouvelle, near forestry sta-

tion, May 1949 (fl), *Rivals s.n.* (TL-R). PITON RAVINE À MALHEUR: heights of Piton de la Ravine à Malheur, 900 m, May 1943 (st), *Rivals s.n.* (TL-R). PLAINE D'AFFOUCHES: forest along path to Plaine d'Affouches, 900 m, May 1943 (st), *Rivals s.n.* (TL-R). ROCHE ECRITE: path to Roche Ecrute, 28 Feb. 1975 (fl), *Coode 5000* (K, 2 sheets; REU); 5 Oct. 1938 (st), *Rivals s.n.* (TL-R). PLAINE DES CAFRES: Plaine des Cafres (st), *Cordemoy s.n.* (TL-R); Piton Bleu, 26 Sept. 1882 (st), *Cordemoy s.n.* (TL-R). PLAINE DES CHICOTS: near Mamode Camp, 1,200 m, 27 Dec. 1966 (st), *Cadet 595* (REU). PLAINE DES MAKES: Domainial line above Tévelave, along edge of Plaine des Makes, Oct. 1943 (st), *Rivals s.n.* (TL-R); ravine of the Col à Maison Rouge, 28 June 1967 (st), *Cadet 1039* (REU). PLAINE DES MERLES: Salazie, 1,200 m, 19 Feb. 1944 (fl), *Rivals s.n.* (TL-R). PLAINE DES PALMISTES: Petite Plaine above Plaine des Palmistes, cloud forest, 1,200 m, 25 Feb. 1979 (fl), *Lorence & Rolland 2454* (MO); 13 Jan. 1973 (fl, fr), *Cadet 4021* (REU). SAINTE ANNE: above Sainte Anne, 1,200 m, 30 May 1974 (fr), *Cadet 4714* (REU); near Sainte Anne bridge (st), *Cordemoy s.n.* (TL-R). TAKAMAKA: Takamaka forest, Ilet à Bananes, 600–1,000 m, 10 Mar. 1979 (fl), *Lorence & Rolland 2525* (MAU, MO); (fl), *Lorence & Rolland 2526* (MO); (fl), *Lorence & Rolland 2527* (MAU, MO); (fl, fr), *Lorence & Rolland 2528* (MAU, MO); (fl), *Lorence & Rolland 2529* (MO); (fl, fr), *Lorence & Rolland 2530* (MAU, MO); path to Bras Cabot, slopes of the Ilet de Patience, 1,200–1,500 m, Feb. 1971 (fl), *Bosser 20578* (P); Grand Fond forest, Takamaka, 900 m, 23 July 1943 (st), *Rivals s.n.* (TL-R). WITHOUT PRECISE LOCALITY: 1836–1837 (fl), *Gaudichaud s.n.* (P); (st), *Rivals s.n.* (TL-R).

Both the upland and lowland forms of *Tambourissa elliptica* subsp. *elliptica* include individuals with either pink or pale greenish to yellowish white floral color morphs (as does subsp. *micrantha*), but never dark purple as in *T. crassa*. Floral odors of both *T. elliptica* subsp. *elliptica* and *T. crassa* are strong and rancid-fruity with overtones of butyric acid, never pleasantly sweet-fruity as in subsp. *micrantha*. In addition, gynoeceous flowers of both subspecies of *T. elliptica* and also of *T. crassa* are morphologically similar and produce a mucilaginous exudate that partly fills the floral cup. Strong similarities in the floral construction of all three Réunion taxa suggest a fairly recent derivation from a single, common ancestor. Both species belong to Group 2A.

Although upland and lowland forms of *Tambourissa elliptica* subsp. *elliptica* are quite distinct in their extremes, they intergrade gradually and clinally. For example, collections from Takamaka (eastern Réunion) form a continuous series ranging from lowland wet forest at 600–700 m elevation, to the lower limits of cloud forest at 900–1,000 m (*Lorence & Rolland 2525–2530*, all MO). Both forms are diploids with $n = 19$. Because they are not separable by any single con-

stant character, nor even by any constant constellation of characters, it is not possible to recognize them formally as taxa. The type of subsp. *elliptica* from the Hauts de la Rivière des Galets (*Boivin s.n.*, P) represents an intermediate form, although most closely approaches the upland type.

Vernacular names. Bois de bombarde, Bois de bombarde à grandes feuilles (Réunion).

13b. *Tambourissa elliptica* subsp. *micrantha*

Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 298, pl. 2, fig. 8. 1982. TYPE: Réunion. Brûlé de Baril: lower montane wet forest, ca. 300 m, 2 Mar. 1979 (fl), Lorence, Lorence & Cadet 2489 (holotype, MO; isotypes, K, MAU, P, REU, Z).

T. quadrifida sensu Cordem., Fl. Réunion 301. 1895 non Sonn.

Monoecious canopy tree 10–12 m tall and 30 cm D.B.H., the bark soft, pale yellow-brown, corky and peeling, the new growth with sparse, short simple hairs, soon glabrous, the mature leafy stems 2–5 mm diam. (to 8 mm diam. on suckers), longitudinally striate. Leaves glabrous, opposite to subopposite, petiolate; petioles (8–) 10–20 mm by 1.5–2 mm; lamina chartaceous to subcoriaceous, elliptic, narrowly elliptic, oblong or obovate-elliptic, (50–)80–180(–220) mm by (15–)25–50(–65) mm, the apex shortly acuminate, shortly acute, obtuse or rarely rounded, the base acutely cuneate to acutely decurrent, the secondary veins (5–)7–12 pairs, making a 55–65° angle with the costa, the venation prominent, finely reticulate, visible to 4(–5°) adaxially and to 5(–6°) abaxially, the margin plane to slightly revolute; juvenile and sucker leaves heterophyllous, long and narrowly elliptic, the lamina attaining 180 mm by 40 mm, the apex acute to acuminate, the secondary veins 10–14 pairs, the petiole and costa bright red when living. Inflorescence ramiflorous on old or new stems, or axillary, a unisexual or sexually mixed pleiochasium of 3–7 flowers, with sparse scattered hairs, the floral axis 8–20 mm by 1–1.5 mm, subtended by several minute, ciliate naviculate bracteoles 0.6–0.8 mm long, or the flowers rarely solitary. Androecious flower in bud globose to globose-depressed, 7–9 mm diam., the apex with 4 minute, obtuse tepals, the pedicel 10–28 mm by 1 mm, subtended by a minute bracteole; at anthesis (3–)4-fid, 16–26 mm diam., the lobes spreading flat; stamens 65–95, ligulate, 1.5–2.5 mm long,

0.5–0.8 mm wide, the filament short, the loculi lateral, comprising ca. $\frac{2}{3}$ – $\frac{3}{4}$ total length of the stamen, apically connivent or confluent, the connective not prolonged. Gynoecious flower in bud napiform-depressed, apiculate with 4 minute tepals, the pedicel (5–)10–20 mm by 0.6–0.8 mm, subtended by a single bracteole; at anthesis 6–7 mm diam. by 4–6 mm long, the orifice X-shaped, 1–2 mm diam., splitting into 4 suberect deltoid lobes; styles numerous, ca. 150–160, short, bluntly columnar, 0.5 mm long by 0.3–0.4 mm wide, interspersed with rare, scattered hairs. Fruiting receptacle solitary or in clusters of 2–3 on leafless branches, cupuliform-urceolate, 25–45 mm diam. by 15–30 mm long, the orifice 6–14 mm diam., comprising ca. $\frac{1}{3}$ – $\frac{1}{2}$ total width of the fruit, subentire, the walls 10–15 mm thick, the external surface dark reddish brown mottled with pale corky patches, the internal surface with scattered, short, bluntly columnar-polyhedral styles ca. 0.3–0.5 mm long by 0.5 mm wide, interspersed with rare, scattered hairs, the pedicel and peduncle 12–16 mm by 3–6 mm. Mature carpels 9–11 mm long, 5–7 mm wide, 3–4 mm thick, the endocarp pale brown, the surface with rugose striations. Gametic chromosome number: $n = 19$. Figure 32.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. *Tambourissa elliptica* subsp. *micrantha* is occasional to locally common from ca. 300 to 700 m in the southern sector of Réunion on the lower slopes of the active volcano, the Piton de la Fournaise (le Volcan) massif (at Basse Vallée, Brûlé de Baril, Forêt de la Mare Longue, Mare d'Arzul, and Bois Blanc). Collections are also known from l'Echo below Plaine des Palmistes (ca. 700 m), and the subspecies reaches ca. 1,000 m at Brûlé de St. Denis and Plaine d'Affouches.

RÉUNION. BOIS BLANC: 300 m, Apr. 1949 (fl), *Rivals s.n.* (TL-R). BRÛLÉ DE ST. DENIS: rainy season (Dec.–Feb.) 1945 (fr), *Rivals s.n.* (TL-R). BASSE VALLÉE: Béloni, 21 Oct. 1971 (fr), *Friedmann* 3265 (P). BRÛLÉ DE BARIL: 26 Feb. 1975 (fl), *Coode et al.* 4963 (K, 2 sheets; REU); 300 m, 2 Mar. 1979 (st), Lorence, Lorence & Cadet 2487 (MAU, MO); (fl), Lorence, Lorence & Cadet 2488 (B, K, MAU, MO, P, REU, Z); 13 July 1979 (fr), Lorence & Cadet 2741 (MO); (fr), Lorence & Cadet 2742 (MAU, MO); (fr), Lorence & Cadet 2743 (B, K, MAU, MO, P, REU, Z). DOS D'ANE: 1,200 m, Mar. 1974 (fl), *Friedmann* 2299 (P, intermediate form). GRAND ÉTANG: (E Réunion) ca. 500 m, 15 July 1979 (fl), Lorence & Rolland 2758 (MO, intermediate form). L'ECHO: St. Benôit to Plaine des Palmistes route, 700 m, 4 July 1967 (st), *Cadet* 1038 bis (REU); (st), *Cadet*

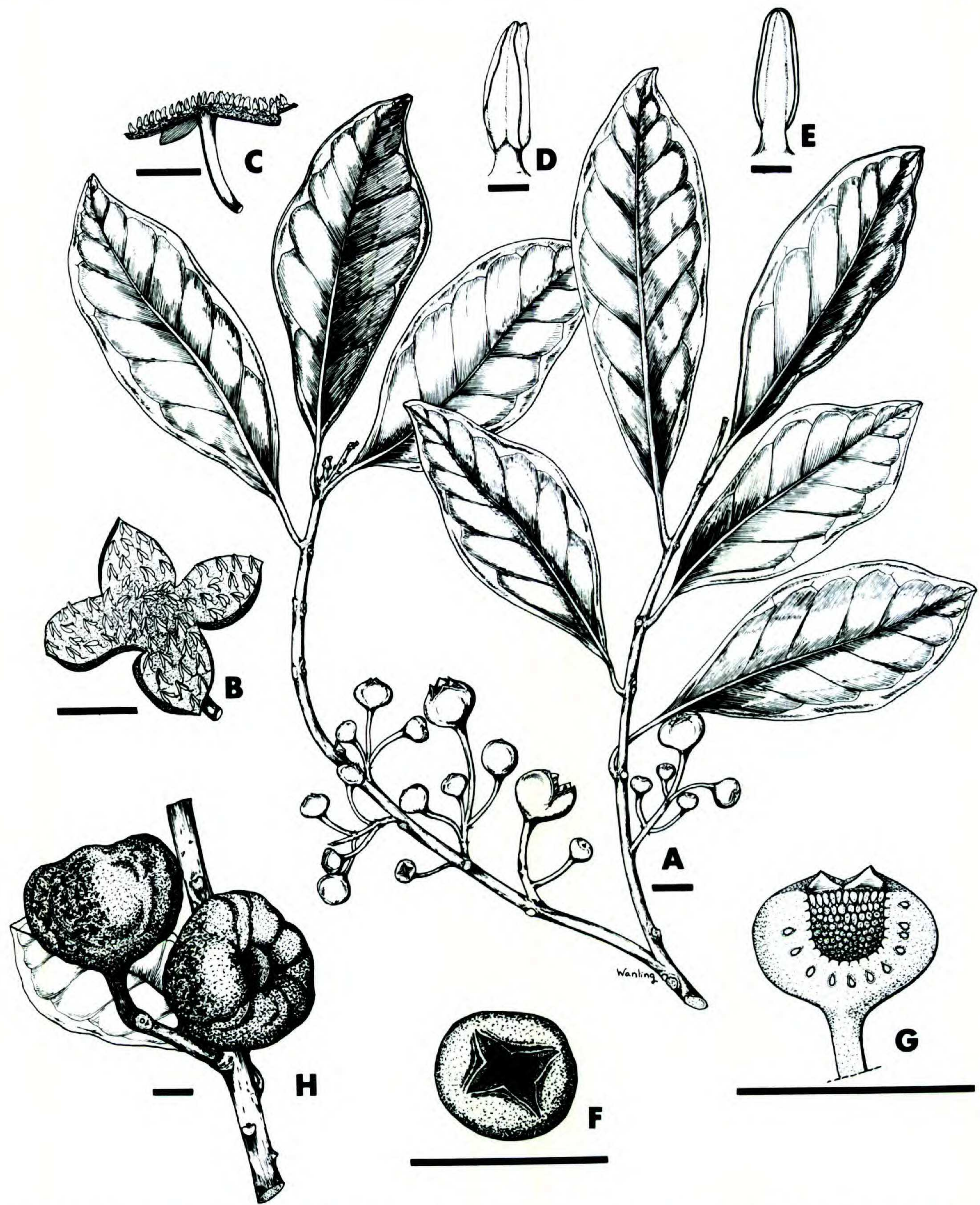


FIGURE 32. *Tambourissa elliptica* (Tul.) A.DC. subsp. *micrantha* Lorence.—A. Habit.—B. Androecious flower at anthesis, apical view.—C. Androecious flower at anthesis, lateral view.—D. Stamen, abaxial view.—E. Stamen, adaxial view.—F. Gynoeceous flower at anthesis, apical view.—G. Gynoeceous flower at anthesis, longitudinal section.—H. Submature fruiting receptacles. A–G. Lorence 2489 (MO). H. Lorence 2741 (MO). Bars equal 10 mm in A–C, F–H, and 1 mm in D, E.

1039 bis (REU, intermediate form); 27 Feb. 1979 (st), Lorence 2462 (MO, intermediate form). PLAINE D'AFFOUCHE: La Montagne, road to Plaine d'Affouches, 1,000 m, pk 4.5, 27 Dec. 1966 (st), Cadet 612 (REU); (fr), Rivals s.n. (TL-R). RIVIÈRE DES REMPARTS: high valley of the Rivière des Remparts, 1,000 m, 7 Mar. 1975 (fl), Cadet 5123 (REU, intermediate form); 1,100 m, (fl), Cadet 5124 (REU, intermediate form). ST. PHIL-

IPPE: Mare d'Arzul forest, 9 Dec. 1943 (st), *Rivals s.n.* (TL-R); St. Philippe (st), *Rivals s.n.* (TL-R); Mare Longue forest, 400–780 m, 14–15 Jan. 1975 (fr), *Bernardi 15044* (G, 3 sheets; P, REU); ca. 500 m, 25 Feb. 1975 (fl), *Coode et al. 4956* (K, 2 sheets; REU); 250–500 m, 2 Mar. 1979 (fl), *Lorence, Lorence & Cadet 2483* (MAU, MO); Jan. 1949 (st), *Rivals s.n.* (TL-R); May 1943 (st), *Rivals s.n.* (TL-R). TAKAMAKA: Takamaka forest, Ilet à Bananes, ca. 800–900 m, 10 Mar. 1979 (fl), *Lorence & Rolland 2524* (MO, intermediate form). WITHOUT PRECISE LOCALITY: 1853–1863 (fl, fr), *Frappier 4* (P, 5 sheets).

At Brûlé de Baril, *Tambourissa elliptica* subsp. *micrantha* becomes a subcanopy or canopy tree attaining 10–12 m with a straight trunk attaining 25–30 cm D.B.H. and a narrow, compact crown with numerous, erect branches. It differs most conspicuously from subsp. *elliptica* in having elliptic to narrowly elliptic leaves with a laminar length to width ratio exceeding 2:1 and often approaching 3:1. Juvenile and sucker leaves of subsp. *micrantha* are longer and narrower than its adult leaves, have more numerous secondary veins, bright red petioles and midribs when living, but lack dentate margins. Subspecies *elliptica* has instead apically dentate-serrate juvenile leaves, as do most other congeners for which data is available.

Flowers of both sexes are conspicuously smaller than in subsp. *elliptica*, hence the epithet *micrantha*. Large individuals of subsp. *micrantha* are monoecious, often with sexually mixed pleiochasia, whereas sex expression appears to be size and/or age related in subsp. *elliptica*. Flowers of subsp. *micrantha* are generally pleiochasial and ramiflorous or axillary, whereas those of subsp. *elliptica* tend to be cauliflorous, sometimes axillary. Fruits of subsp. *micrantha* are generally smaller, often produced in clusters of two or three on the branches, and are more conspicuously mottled in contrast to the larger, solitary and often caulinary fruits of subsp. *elliptica* which are more uniformly pale brown.

Although the two subspecies of *Tambourissa elliptica* occur together in certain areas of wet forest at low to medium altitudes (e.g., Hauts du Bois Blanc; Hauts du Brûlé de St. Denis) and remain distinct there, they intergrade in other localities, e.g., Takamaka (*Lorence & Rolland 2524*, MO), Dos d'Ane (*Friedmann 2299*, P), Rivière des Remparts (*Cadet 5123, 5124*, REU), and Grand Etang (*Lorence & Rolland 2758*, MO). Both subspecies have $n = 19$. Despite occasional intermediate collections, the two taxa are separable by relatively constant, modally distinct

characters of floral size and odor, staminal length and number, ratio of laminar length to width, and fruit size. I have therefore chosen to recognize them as subspecies.

Tambourissa elliptica subsp. *micrantha* belongs to species Group 2A. In view of its monoecy, less reduced pleiochasial inflorescences, and flowers intermediate in size and number of parts, it seems to be the least specialized of the Réunion taxa and therefore probably most like the ancestral species from which the others were derived.

Vernacular names. Bois de bombarde, Bois de bombarde à petites feuilles (Réunion).

- 14. *Tambourissa crassa*** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 298, pl. 2, fig. 7. 1982. TYPE: Réunion. Road to Maïdo above Petite France, on forestry road C.F. 81; low cloud forest, ca. 1,200–1,400 m, 19 July 1979 (fl), *Lorence 2780* (holotype, MO; isotypes, K, MAU, P, REU, Z).

T. religiosa sensu Cordem., Fl. Réunion 301. 1895 non (Tul.) A.DC.

Dioecious tree, rarely shrubby, 7–8 m tall, the trunk stout, to 30 cm D.B.H., the bark pale grayish brown, smooth to irregularly fissured-flaking, the crown compact, the new growth glabrous, rarely with a few scattered hairs, the mature leafy stems 4–9 mm diam., terete, glabrous, longitudinally wrinkled. Leaves glabrous, opposite to subopposite, petiolate to subsessile; petiole stout, 4–15(–20) mm by (2–)3–6 mm; lamina coriaceous, obovate, broadly obovate, broadly elliptic or suborbiculate, (40–)60–175 mm by (20–)40–140 mm, the apex obtuse, rounded, or retuse-emarginate, the base acutely cuneate to acutely decurrent, the secondary veins 5–6 pairs, making a 45–55° angle with the costa, the venation obscure, visible to 2(–3°) adaxially and to 3(–4°) abaxially, the margin moderately revolute, the color pale brown to bright yellow-green when dry. Inflorescence a solitary monochasium terminal on the leafy stems (the subtending leaves $\pm$ caducous), or rarely cauliflorous or ramiflorous and terminal on short, leafy or leafless bracteate shoots. Androecious flower in bud globose, 13–14 mm diam., glabrous, apiculate with 4 small, obtuse-deltoid, $\pm$ glabrous tepals, the pedicel and peduncle stout, erect or recurved, 15–32 mm by 4–5 mm, bearing several caducous,

ciliate deltoid bracteoles basally; at anthesis 4–5-fid, 32–45(–50) mm diam., the lobes thick, spreading almost flat or somewhat incurved, the internal receptacle surface glabrous; stamens numerous, ca. 125–250, ligulate-ellipsoid, 4–5 mm long by 1–1.5 mm wide, the filament short and thickened basally, the loculi lateral, comprising ca. $\frac{2}{3}$ – $\frac{3}{4}$ total length of the stamen, usually confluent apically, occasionally free, the connective not prolonged. Gynoecious flower in bud napiform to globose-depressed, the apex with 4 small, obtuse or deltoid, glabrous or sparsely ciliate tepals, the pedicel and peduncle suberect, 8–25 mm by 2–4 mm, bearing several small, $\pm$ ciliate bracteoles basally; at anthesis urceolate-globose to urceolate-napiform, 12–14 mm diam. by 8–10 mm long, the walls thick, the apex splitting into 4(–8) thick, subequal, shallowly deltoid lobes, the orifice 5–6 mm diam., comprising ca. $\frac{1}{4}$ – $\frac{1}{3}$ total width of the receptacle; styles numerous, ca. 200 or more, crowded, bluntly columnar, ca. 0.5 mm long by 0.3–0.5 mm wide, the internal receptacle surface glabrous, producing a mucilaginous exudate. Submature fruiting receptacle globose-urceolate, ca. 60 mm diam. by 40 mm long, corky brown externally, internally glabrous with numerous scattered, bluntly columnar polyhedral styles ca. 0.3 mm long by 0.5–0.8 mm wide, the pedicel and peduncle stout, ca. 50 mm by 10 mm. Mature carpels unknown. Figure 33.

Distribution. Endemic to Réunion (Fig. 31).

Habitat. *Tambourissa crassa* is local and occasional in cloud forest formations from ca. 1,200 to 2,000 m, rarely extending as low as 700 m (e.g., at Basse Vallée, *Bosser 21313*).

RÉUNION. BASSE VALLÉE: humid forest, 600–700 m, 20 Oct. 1972 (fr), *Bosser 21313* (P). BOIS DE NÈFLES: Hauts du Bois de Nèfles, St. Paul, 1,400 m, 17 Sept. 1979 (fl, fr), *Cadet 4790* (REU); (fl), *Cadet 4791* (REU). LES MARES: Les Mares, 1,500 m (fl), *Friedmann 3001* (P). MAÏDO: road to Maïdo above Petite France, 1,350 m, 22 Feb. 1979 (st), *Lorence & Cadet 2412* (MAU, MO); ca. 1,200 m, 22 Feb. 1979 (st), *Lorence & Cadet 2414* (MAU, MO). PLAINE DES CAFRES: (st), *Cordemoy s.n.* (TL-R); Col de Bellevue at Grande Montée de la Plaine des Cafres, low cloud forest, 1,600 m, 27 Feb. 1979 (fl), *Lorence 2468* (MAU, MO); (fl), *Lorence 2469* (MAU, MO); (fl), *Lorence 2470* (MO); 17 July 1979 (fl), *Lorence 2767* (K, MAU, MO, P, Z); summit of the slopes of the Grande Montée, 15 Mar. 1943 (st), *Rivals s.n.* (TL-R). PLAINE DES MAKES: 16 Mar. 1971 (st), *Friedmann 1031* (P). PLAINE DES PALMISTES: banks of the Ravine Petite à Bras des Calumets, 1,300 m, 17 Jan. 1972 (fl), *Cadet 3477* (REU). PLAINE DES SALAZES: 2,000 m, 19 Feb. 1944 (st), *Rivals s.n.* (TL-R). PLAINE DES TAMARINS: 1,800 m, below the Col de Fourche,

Maïfate, 28 Nov. 1974 (fl), *Cadet 4604* (REU). RIVIÈRE DE L'EST: low thicket along the Rivière de l'Est, 1,550 m, Nov. 1967 (fl), *Cadet 5717* (REU). TÉVELAVE: forestry road above Tévelave, cloud forest, 1,300–1,400 m, 28 Feb. 1979 (fl), *Lorence 2478* (MO); along the domainial line, 1,700 m, cloud forest transitional to heath formation, 6 Mar. 1979 (fl), *Lorence 2500* (MAU, MO); Hauts du Tévelave, 1,500–1,900 m (st), *Rivals s.n.* (TL-R). WITHOUT PRECISE LOCALITY: (st), *Rivals s.n.* (TL-R).

Tambourissa crassa belongs to species Group 2A and is most closely allied to *T. elliptica* subsp. *elliptica*, also from Réunion, from which it can be distinguished by its truly dioecious habit, thicker leaves, and solitary, terminal flowers and fruits borne at the ends of the top branches (rarely caulinary on short, leafy or leafless bracteate shoots, but even then solitary and terminal). The succulent, strongly discolored leaves of *T. crassa* have a well-developed hypodermis 4–6 cell layers thick, which is only 2–3 cells thick in both subspecies of *T. elliptica*. Other distinguishing features are its somewhat pachycaulous habit, sparse and compact crown, the almost camphor-like fragrance of the dried specimens, and absence of stone cells and tanniferous idioblasts from the floral ground tissue.

Unlike the more variable *Tambourissa elliptica* subsp. *elliptica*, *T. crassa* is quite stable morphologically. As in most species, a certain amount of intraspecific variation occurs in leaf size and shape, flower color, and number of stamens, but both species are quite distinct morphologically. Both *T. crassa* and *T. elliptica* subsp. *elliptica* frequently occur sympatrically in the cloud forest zone (1,200–2,000 m), e.g., at Hauts du Tévelave, and along the road to Maïdo, where neither intermediates nor putative hybrids were found. For these reasons I regard *T. crassa* as a discrete species rather than a subspecies of *T. elliptica* in spite of certain morphological similarities.

Both *Tambourissa crassa* and *T. elliptica* subsp. *elliptica* have large, structurally similar leaves and large flowers with numerous stamens and styles, which are presumably adaptations to a shared habitat and similar pollinators. Apparently both taxa have evolved from a common ancestor with less specialized features, which *T. elliptica* subsp. *micrantha* appears to approach most closely. *Tambourissa crassa* has attained the highest degree of specialization of the three Réunion taxa, however, in being dioecious and having inflorescences reduced to a single, terminal flower.

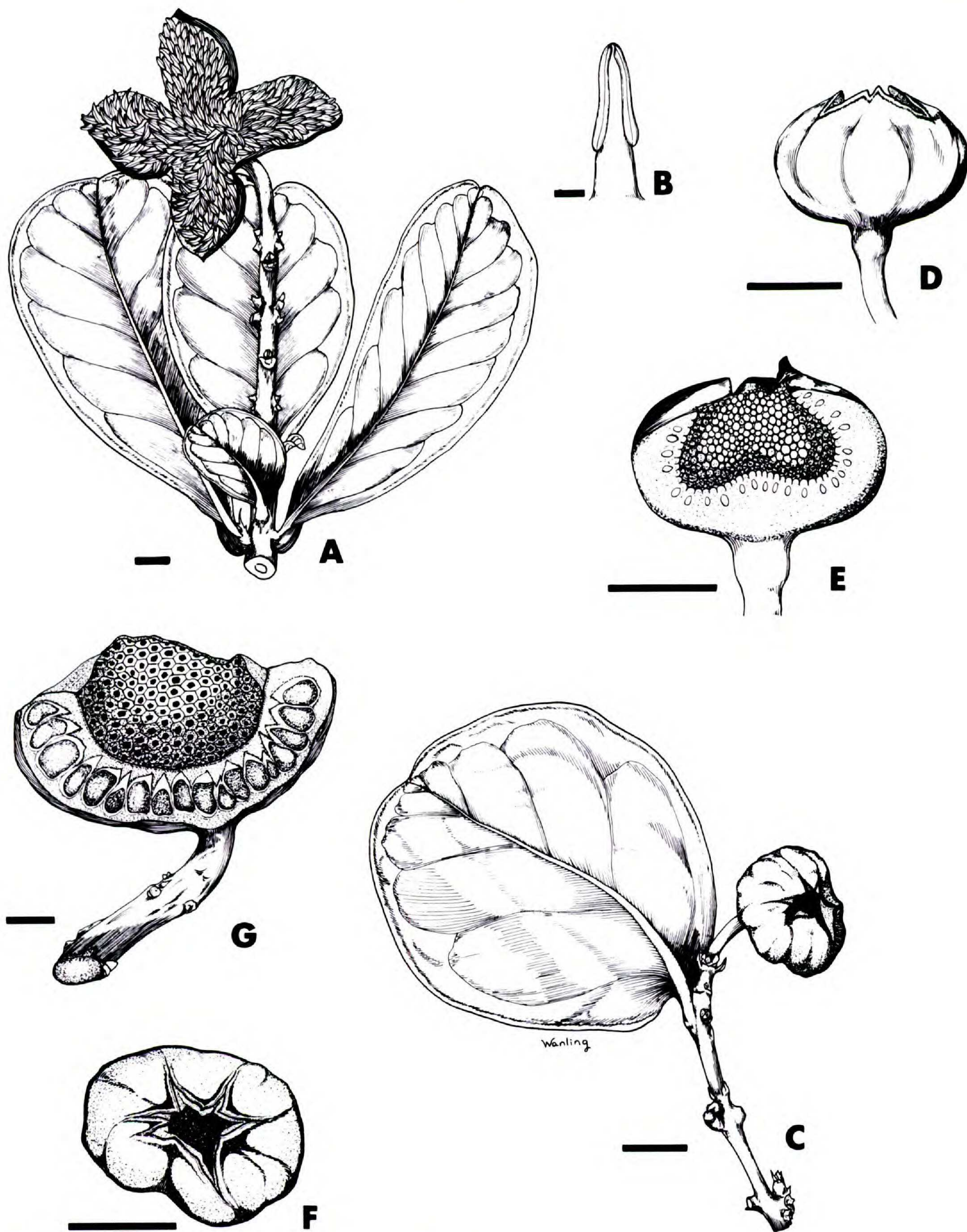


FIGURE 33. *Tambourissa crassa* Lorence. — A. Habit, with androecious flower at anthesis. — B. Stamen, adaxial view. — C. Habit, with gynoecious flower at anthesis. — D. Gynoecious flower at anthesis, lateral view. — E. Gynoecious flower at anthesis, longitudinal section. — F. Gynoecious flower at anthesis, apical view. — G. Fruiting receptacle, longitudinal section. A, B. Lorence 2767 (MO). C–F. Lorence 2780 (MO). G. Cadet 4790 (REU). Bars equal 10 mm in A, C–G, and 1 mm in B.

Flowers of both sexes produce strong, rancid-fruity floral odors of butyric acid, as do those of *Tambourissa elliptica* subsp. *elliptica*. Both pale yellow-green and dark purple floral color morphs occur, although flower color appears to be constant within a given population (e.g., yellow at Col de Bellevue, purple at Hauts du Tévelave).

Vernacular names. Bois de bombarde, Bois de bombarde à grandes feuilles (Réunion).

15. *Tambourissa comorensis* Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 295, pl. 1, figs. 3, 4. 1982. TYPE: Comore Archipelago. Grande Comore: La Grille forest above Maoueni, ca. 800 m, 29 July 1979 (fl, fr), Lorence & Banfi 2878 (holotype, MO; isotypes, B, G, K, MAU, P, REU, Z).

Large monoecious canopy tree 15–20 m tall and 50 cm D.B.H., the bark pale brown, smooth, flaking, the new growth glabrous or with rare, scattered hairs, the mature leafy stems pale greenish, terete, glabrous, 3–4 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petiole 10–28 mm by 1–1.5 mm; lamina chartaceous, elliptic, narrowly elliptic, ovate, oblong or lanceolate, (60–)80–140 mm by (20–)30–75 mm, the apex shortly acuminate, rarely acute or obtuse, the tip rounded, the base acutely cuneate to obtuse, generally slightly decurrent, the secondary veins 4–7 pairs, making a 50–60° angle with the costa, the venation prominent, visible to 4(–5°) on both surfaces, the margin plane to slightly revolute; juvenile leaves heterophyllous, the apical $\frac{1}{2}$ – $\frac{2}{3}$ of the lamina serrate-dentate with 1–5 pairs of large teeth, the petiole red when living. Inflorescence cauliflorous or ramiflorous, on meristematic swellings on the trunk or on leafless nodes of the branches, a short, unisexual or sexually mixed pleiochasium of 4–9 flowers, the floral axis 5–20(–60) mm by 2–3 mm, when young finely velutinous-pubescent with short, simple or fasciculate hairs, each pedicel subtended by a minute naviculate bracteole. Androecious flower in bud globose, 9–14 mm diam., externally puberulent to glabrous, $\pm$ pustular, apiculate with a small pore flanked by 2–4 pairs of dark, hirsutulous, broadly deltoid tepals, the pedicel 8–30 mm by 1–1.5 mm; at anthesis deeply 4(–6)-fid, 23–35 mm diam., the lobes spreading flat and reflexing slightly, the apex of each lobe with several fleshy tepals internally, the internal receptacle surface glabrous; stamens nu-

merous, ca. 125–150, linear-ligulate, 2.5–4 mm long by 0.7–1 mm wide, the loculi separate, parallel, lateral or slightly abaxial, occupying almost the entire length of the stamen, the filament short, thick, the connective not prolonged. Gynoecious flowers 1–6 per inflorescence, terminal or lateral, the pedicel 12–20 mm by 2 mm; at anthesis broadly patelliform-urceolate, 12–15 mm diam. by 5–7 mm long, the orifice circular, entire, 7–10 mm diam., comprising $\frac{2}{3}$ total width of the receptacle, the rim velutinous, open even in bud, the external surface puberulent, $\pm$ pustular; styles numerous, several hundred, coalescent, short, bluntly columnar-polyhedral, 0.3–0.5 mm long and wide, the apex papillose, the internal receptacle surface with scattered hairs. Fruiting receptacle solitary or in clusters of 2–3 on the trunk and major branches, irregularly cupuliform, often $\pm$ distorted, 90–175 mm diam. by 50–75 mm long, the orifice comprising ca. $\frac{1}{3}$ – $\frac{1}{2}$ total width of the receptacle, entire, subcircular, 45–90 mm diam., the walls 16–25 mm thick, externally smooth, mottled reddish brown, internally glabrous with numerous scattered columnar-polyhedral styles 0.3–0.4 mm long by 0.5–0.8 mm wide. Mature carpels ovoid to ellipsoid, compressed, 11–13 mm long, 5–8 mm wide, 4–6 mm thick, the endocarp dark brown to black, the surface scrobiculate. Gametic chromosome number, $n = 19$. Figure 34.

Distribution. Endemic to Grande Comore (Fig. 35).

Habitat. *Tambourissa comorensis* occurs in lower montane wet forest formations. All known collections are from La Grille forest above Maoueni (northern part of the central ridge, 800–900 m), and from forest above Ntsorale Dimane along the eastern part of the same massif (250–900 m, fide Bernardi). At La Grille, I found it to be locally abundant and codominant as a subcanopy or canopy tree, striking when in fruit with numerous, large brown receptacles hanging from the trunk and branches, some split open to reveal an array of red-orange carpels set against a pale orange background. One of the largest known members of the genus, both in habit and in fruit, it flowers from August to December concurrently with the ripening of the previous year's fruit crop.

GRANDE COMORE. NTSORALE DIMANE: 250–900 m, *Nuxia* and *Weinmannia* formation, 9 Dec. 1967 (fl), Bernardi 11803 (G, 2 sheets; K, P, Z). LA GRILLE: 850–900 m, *Tambourissa*, *Ocotea*, *Anthocleista*, and *Polyscias* formation, 1–3 Dec. 1967 (fl, fr), Bernardi 11645 (G, 2 sheets; K, P, Z); May 1963 (fl), Bosser 18096

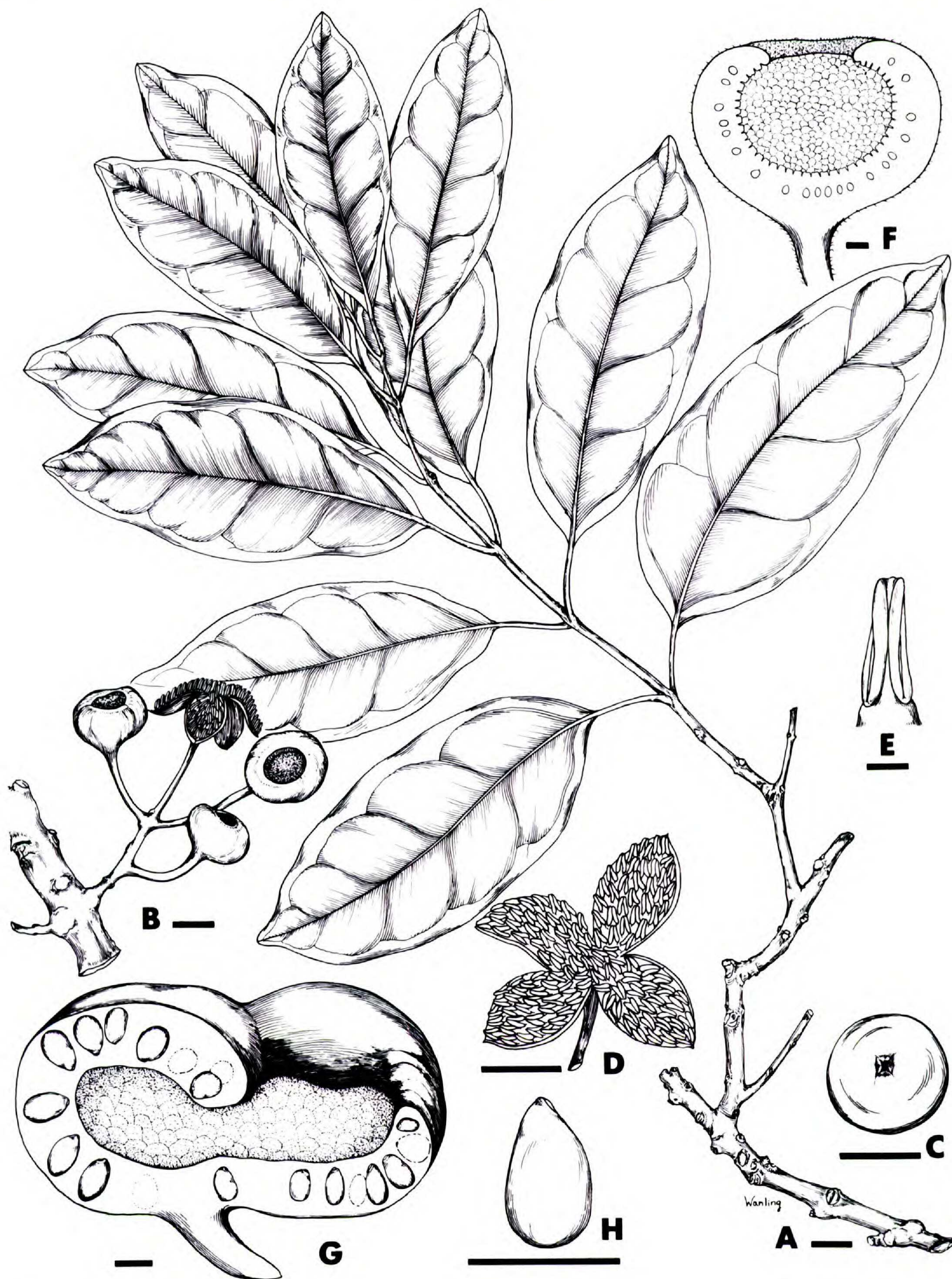


FIGURE 34. *Tambourissa comorensis* Lorence. —A. Habit. —B. Inflorescence with androecious and gynoecious flowers. —C. Androecious flower in bud, apical view. —D. Androecious flower at anthesis, apical view. —E. Stamen, adaxial view. —F. Gynoecious flower, longitudinal section. —G. Submature fruiting receptacle, longitudinal section. —H. Fruiting carpel, lateral view. All *Lorence 2878* (MO). Bars equal 10 mm in A–D, G, H, and 1 mm in E, F.

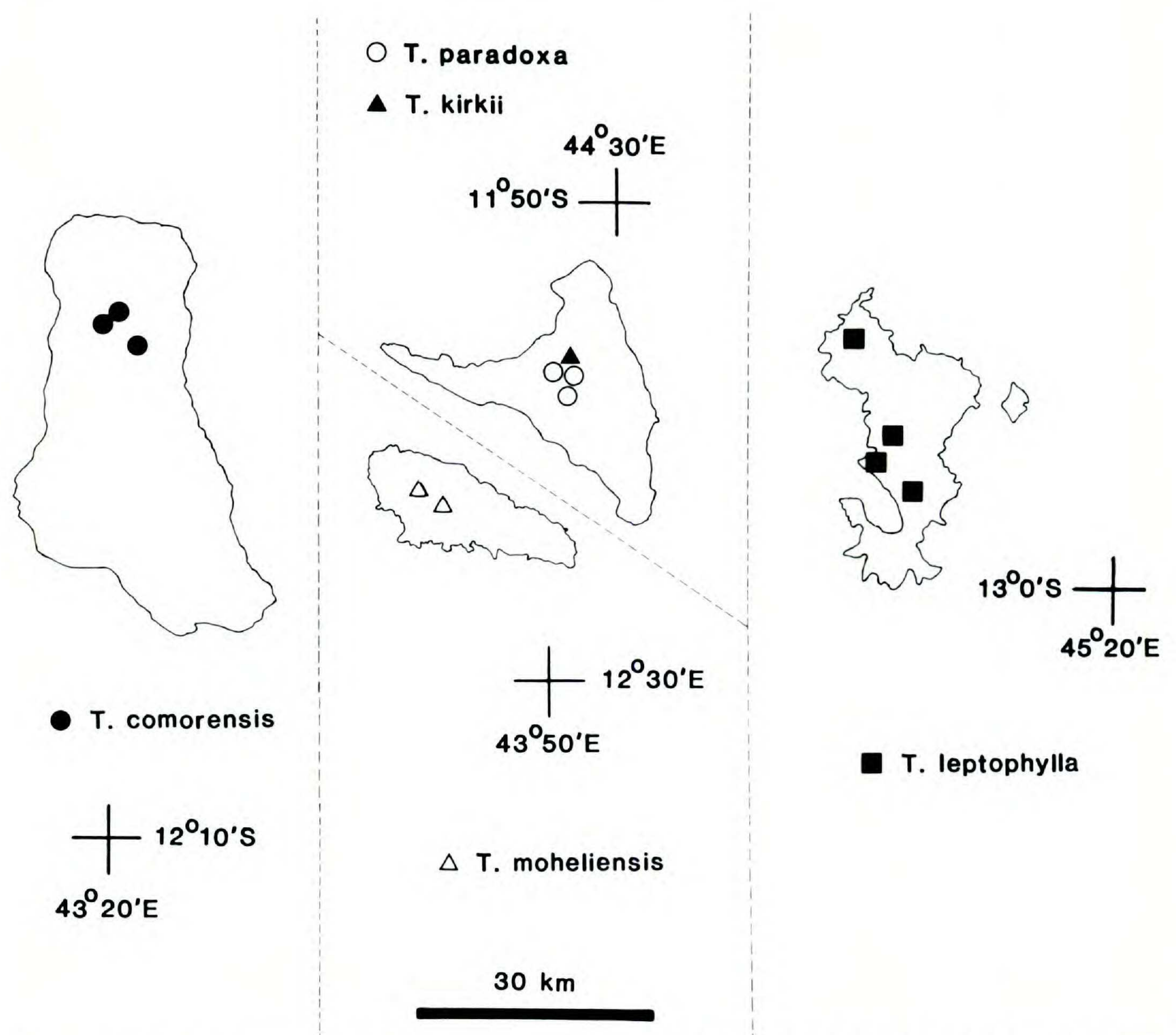


FIGURE 35. Distribution maps of *Tambourissa* in the Comore Islands (left to right): Grande Comore, Mohéli, Anjouan, Mayotte.

(MAD, P); ca. 800 m, 29 July 1979 (fr), *Lorence & Banfi* 2877 (MO, K, P); 9 Feb. 1957 (fl), *Anon. in SF-16529* (P).

Tambourissa comorensis belongs to species Group 2A, also including *T. leptophylla* which differs by its smaller androecious buds, fewer stamens, and by its gynoecious receptacle with a much smaller orifice and acute, conical styles. Also, fruits of the latter are uniformly dull, corky brown externally with a smaller orifice. Dried fruits of *T. comorensis* are strongly fragrant in the herbarium, like those of *T. moheliensis* (Group 3). *Tambourissa kirkii* (Group 2B) differs by its small, globular androecious flowers, which open only partially and contain fewer stamens with acute, prolonged connectives. In living material, androecious flowers of *T. comorensis* are white and produce a pleasant, sweet odor of fer-

menting fruit. Buds and gynoecious flowers are pale green externally. At anthesis, gynoecious flowers have glistening, pale green styles, although massive mucilage production was not apparent. In mixed inflorescences of *Lorence & Banfi* 2788, the gynoecious flowers matured before the androecious flowers.

Vernacular name and uses. M'Bweza (Grande Comore), meaning "to calm the pain" or "to heal." Natives of Grande Comore infuse the leaves to make a medicinal tea.

16. *Tambourissa leptophylla* (Tul.) A.DC., Prodr. 16(2): 658. 1868; Baill., Hist. Pl. ed. 2, 1: 310, 344, 345. 1871; Cavaco in Humbert, Fl. Madagascar 80: 34, fig. VIII:1-4. 1959. *Ambora leptophylla* Tul., Ann. Sci.

Nat. (Paris) 4(3):29. 1855; Tul., Monogr. Monim. 298, tab. 25, fig. 1. 1855. TYPE: Comore Archipelago. Mayotte: Zuaby (ca. 1851) (fl), *Boivin 3133* (lectotype, P, here designated; isoelectotypes, P, 4 sheets).

Monoecious or subdioecious tree attaining 10 m tall and 40 cm D.B.H., the bark pale brown, flaking, the new growth finely pubescent, the mature leafy stems glabrescent, terete, 3–5 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petiole 15–20 mm by 1.5–2.5 mm; lamina membranaceous to chartaceous, ovate to elliptic or oblong, 120–250 mm by 60–110 mm, the apex shortly acuminate to acute, the base acute to obtuse, often slightly decurrent, the secondary veins 5–8 pairs, making a 50–65° angle with the costa, the venation visible to 4° adaxially and to 4(–5°) abaxially, the margin plane to slightly revolute; juvenile and sucker leaves heterophyllous, the margin serrate with 2–5 pairs of teeth in the apical half, the petioles red when living. Inflorescence a pleiochasium or thyrses of 7–25 flowers, sometimes leafy, cauliflorous from meristematic swellings on the trunk, or a ramiflorous pleiochasium of 5–11 flowers on the leafless nodes, or the flowers solitary and axillary, when young finely velutinous, later puberulent, the floral axis 20–150 mm by 1–3 mm, subtended by several minute, caducous bracteoles. Androecious flower in bud globose-depressed, 6–8 mm diam., smooth, the apex with 4 minute puberulent tepals, the pedicel 10–40 mm by 1–1.5 mm, subtended by a small, velutinous deltoid bracteole; at anthesis deeply 4-fid, 20–25 mm diam., the lobes spreading flat, the internal receptacle surface glabrous; stamens 80–90, linear-ligulate, recurved, 2–3 mm long by 0.8–1 mm wide, the loculi separate, parallel, occupying almost the entire length of the stamen, apically connivent or the connective slightly prolonged and apiculate. Gynoecious floral receptacle globose-patelliform, apically depressed; at anthesis 10–15 mm diam. by 5–7 mm long, the orifice entire, circular, comprising ca. $\frac{1}{4}$ – $\frac{1}{3}$ total width of the receptacle, open even in bud, the rim hirsute; styles very numerous, ca. 300–600, broadly conical, 0.6–0.8 mm long by 0.3–0.5 mm wide basally, the internal receptacle surface hirsute between the styles. Fruiting receptacle solitary or in clusters of 2–4 on the trunk and major branches, globose-patelliform, apically depressed, 90–130 mm diam. by 75–90 mm long, the orifice circular, entire, 15–40 mm diam., comprising ca. $\frac{1}{6}$ – $\frac{1}{4}$

total width of the receptacle, the walls 16–25 mm thick, the external surface uniformly dull, corky grayish brown, the internal surface with scattered, sharply conical styles 0.7–1 mm long by 0.5–0.8 mm wide basally, interspersed with abundant simple hairs, the pedicel and peduncle tapered, 70–80 mm long by 9–10 mm diam. medially. Mature carpels ovoid-compressed, 13–17 mm long, 8–10 mm wide, 3–6 mm thick, the endocarp light to dark brown, the surface shallowly foveolate-reticulate.

Distribution. Endemic to Mayotte, Comore Archipelago (Fig. 35).

Habitat. It is local and occasional in lower montane evergreen wet forest formations often dominated by *Aphloia* and *Nuxia*. Recent collections are from the Benara massif (400–653 m) and also the Hachiroungou massif (400–600 m), in remnants of indigenous forest. The species also occurs in secondary forest with native remnants, the recent collections being from Barakani and Sada, both at ca. 100 m. Flowering occurs from August to September concurrently with the ripening of last year's fruits.

MAYOTTE. BARAKANI: secondary forest and along roadside, ca. 100 m, 24 July 1979 (fr), *Lorence & Saida 2824* (MO); near Barakani, Aug. 1977 (fl, fr), *Tattersall s.n.* (MO). BENARA MASSIF: E peak, wet forest on summit, ca. 600–653 m, 24 July 1979 (st), *Lorence & Saida 2828* (K, MO); (fl), *Lorence & Saida 2829* (MAU, MO, P). DZOMNOGNE: (fl), *Pobeguain 86* (P). HACHIROUNGOU MASSIF: (NW Mayotte) wet forest with *Nuxia* and *Aphloia*, ca. 400–500 m, 26 July 1979 (fr), *Lorence & Saida 2854* (K, MAU, MO, P, REU, Z). SADA: ca. 100 m, Aug. 1977 (fl), *Tattersall s.n.* (MO).

Tambourissa leptophylla belongs to species Group 2A. Its androecious flowers most closely approach those of *T. comorensis*, which also split into four flat segments and bear numerous stamens with long anthers, although flowers and buds of the latter are larger. Gynoecious flowers of *T. leptophylla* have acutely conical styles as in *T. kirkii* (Group 2B), but androecious flowers of the latter are much smaller, open only partially, and have fewer stamens (ca. 50) with short, medial loculi and acutely prolonged connectives. All three species are presumably derived from a common ancestor, perhaps one similar to *T. madagascariensis*.

Vernacular name. Ambora (Mayotte).

17. *Tambourissa kirkii* Cavaco, Kew Bull. 12(2): 228. 1957; Cavaco, Bull. Soc. Bot. France

104: 284, fig. 3. 1957. TYPE: Comore Archipelago. Johanna (Anjouan): without precise locality, Zambesi Expedition, 1,000 ft. (ca. 300 m), small tree, Aug. 1862 (fl, fr), *Kirk s.n.* (holotype, K) (see also Kirk's fig. 355, with type).

Monoecious shrub or small tree, the new growth hirsutulous, the mature leafy stems glabrous, stramineate, 2.5–4 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles 10–15 mm by 1–1.5 mm; lamina ovate to elliptic, 100–135 mm by 55–70 mm, the apex shortly acuminate, the base obtuse to rounded, the secondary veins 6–7 pairs, making a 50–55° angle with the costa, the venation visible to 3–4° on both surfaces, the margin slightly revolute. Androecious inflorescence unknown. Androecious flower (from Kirk's fig. 355) globose, ca. 9–10 mm diam.; at anthesis deeply 3-fid, opening slightly, the lobes incurved; stamens probably ca. 50, subulate, ca. 3–4 mm long by 0.5 mm wide, the loculi separate, lateral, occupying medial $\frac{1}{3}$ of stamen, the filament basally broad, comprising ca. $\frac{1}{3}$ total length of the stamen. Gynoecious inflorescence a 4(–5)-flowered, finely velutinous pleiochasium, the position unknown, the floral axis ca. 20 mm by 1.5 mm, bearing rare, scattered bracteoles; female floral receptacle cupuliform-patelliform, 8–12 mm diam. by 5–6 mm long, the orifice broad, circular, entire, comprising ca. $\frac{3}{4}$ total width of the receptacle, the rim velutinous, the external surface finely velutinous, $\pm$ pustular; styles numerous, ca. 200, broadly conical, apiculate, 0.5–1 mm long by 0.5 mm diam. basally, bearing short, scattered hairs, the internal receptacle surface velutinous between the styles. Fruiting receptacle (from Kirk's fig. 355) broadly cupuliform-patelliform, ca. 250–300 mm diam., the broad, subcircular orifice comprising ca. $\frac{1}{3}$ – $\frac{2}{3}$ total width of the receptacle, the conical styles persistent in fruit. Mature (?) carpels ca. 10–12 mm long by 7–8 mm wide, ovoid-compressed, the endocarp "black and hard, surrounded with a red fleshy body" (fide Kirk).

Distribution. Endemic to Anjouan (Fig. 35).

Habitat. According to the information given on the label, *Tambourissa kirkii* occurs at 1,000 ft. (ca. 300 m), but on his figure 355 (an unpublished pencil drawing), Kirk notes "shrub growing at height of 2,000 feet (ca. 600 m) . . . seeds said to be cathartic. Monoecious." It probably occurs in montane wet forest.

Tambourissa kirkii belongs to species Group 2B. As noted by Cavaco (1957a), it is closely allied to *T. leptophylla* (Group 2A) from neighboring Mayotte. The latter differs by its more sparsely pubescent inflorescence, smaller gynoecious floral and fruiting receptacle orifice, glabrous styles, and by its androecious flower which is about twice as large with more numerous stamens having much longer loculi extending for almost the entire length of the stamen, and a scarcely prolonged connective.

Tambourissa paradoxa (Group 2B), also from Anjouan, has smaller, globular androecious flowers opening by a small pore and structurally similar stamens: it may even be conspecific with *T. kirkii*. As gynoecious flowers are unknown in the former, however, and androecious flowers of the latter are known only from a single pencil sketch, I have decided to recognize both species until further data and collections become available. *Tambourissa comorensis* and *T. leptophylla* differ by the characters mentioned above.

18. *Tambourissa paradoxa* Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. TYPE: Comore Archipelago. Johanna (Anjouan): without precise locality (fl), *Anon. sub Herb. Blackburn s.n.* (possibly *Bojer*) (holotype, K).

T. johannae Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. TYPE: Comore Archipelago. Johanna (Anjouan): Zylangi Lake, 27 Oct. 1862 (fl), *Anon. sub Zambesi-Expedition s.n.* (possibly *Kirk*) (holotype, K, lefthand specimen with flowers).

Monoecious shrub or small tree attaining 10 m tall, the new growth unknown, the adult leafy stems glabrous, terete, 3–4 mm diam., yellowish brown. Leaves opposite to subopposite, glabrous, petiolate; petioles 10–20 mm by 1–1.5 mm; lamina chartaceous, elliptic to ovate elliptic, 60–140 mm by 25–50 mm, the apex acute to acuminate, the base acutely cuneate to acutely decurrent, the secondary veins 5–8 pairs, making a 40–45° angle with the costa, the venation prominent and visible to 3° adaxially and to 4° abaxially, the margin moderately revolute. Androecious inflorescence ramiflorous, a sparse, puberulent pleiochasium of 3–11 flowers, or the flowers solitary and axillary, the floral axis 6–12 mm by 1 mm, bearing scattered, simple hairs, subtended by several pairs of minute, ciliate deltoid bracteoles. Androecious flower in bud globose, the pedicel 5–12 mm by 0.6–1 mm, bearing a few sparse hairs, subtended by 1(–2) minute,

caducous deltoid bracteoles; at anthesis globose, 4–8 mm diam., not splitting but opening by a shallowly 4-lobed apical orifice ca. 2 mm diam. flanked by 4 small, decussate, obtusely deltoid ciliate tepals ca. 0.6–1 mm wide by 0.3–0.5 mm long, the internal surface of each lobe bearing 2–10 fleshy, obtuse to deltoid tepals intergrading with the stamens; stamens ca. 40–50, subulate-lanceolate, 2–3 mm long by 0.5–0.8 mm wide, the loculi lateral, separate, occupying basal $\frac{2}{3}$ of stamen, the connective prolonged, acuminate, slightly exerted from the orifice at anthesis; internal receptacle surface glabrous. Gynoecious flowers unknown. Fruiting receptacle solitary on leafless branches, shallowly cupuliform, 53–150 mm diam. by 25–50 mm long, externally corky, the orifice comprising ca. $\frac{1}{2}$ total width of receptacle, the internal surface with numerous broadly conical styles 0.7–0.8 mm long, more or less glabrous in between; pedicel and peduncle 15–17 mm by 5–7 mm. Mature carpels ovoid-compressed, 11 mm long by 6 mm wide.

Distribution. Endemic to Anjouan (Fig. 35).

Habitat. The species is apparently restricted to evergreen montane wet forest from ca. 650 to 1,400 m, according to available information.

ANJOUAN. WITHOUT PRECISE LOCALITY: Traprock (?) soils of hills, 2,000–3,000 ft., 29 Oct. 1862 (st), *Anon. sub Zambesi Expedition s.n.* (possibly *Kirk*) (K, sterile right hand specimen, not a type); (fl), *Levanché 21* (P); Oct. 1902 (fl, fr), *Levanché s.n.* (P); forêts, May 1850 (st), *Boivin s.n.* (P). N'TNIGUE PEAK: 4,200 ft. (ca. 1,400 m), in evergreen forest, food of pigeons, bulbuls and thrushes, tree $\pm$ 20 ft. tall with huge fruits hanging on stem filled with orange covered black seeds, 2 Oct. 1958 (fr), *Benson 142* (BM).

The types of *Tambourissa johannae* and *T. paradoxa* are both from Anjouan. Both collections have morphologically similar leaves, small, globular androecious flowers which open by a narrow apical orifice flanked internally by decussate, scale-like tepals, and have virtually identical stamens containing oil cells and a few sclerids, but lacking tanniferous idioblasts. It seems clear that these two concurrently published taxa are conspecific. I have chosen to retain the epithet *paradoxa*, as its type possesses more numerous and mature flowers than the type of *T. johannae*. *Tambourissa paradoxa* is an imperfectly known species and further field observations and collections, particularly of female flowers and fruit, are desired.

As is the case for *Tambourissa gracilis* and *T. purpurea* (both Madagascar), the androecious

flowers of *T. paradoxa* open by small apical pores. Unlike the stamens of the former two, which are nearly sessile with apically confluent loculi, those of *T. paradoxa* are long and lanceolate with separate, lateral loculi and acute, prolonged connectives.

A close affinity appears to exist between *Tambourissa paradoxa* and *T. kirkii* (also Anjouan), which has strikingly similar floral and staminal morphology, although androecious flowers of the latter species split into 3–4 segments and lack the exerted connectives of the former. Both belong to species Group 2B. Similar androecious floral and staminal morphology occurs in *T. moheliensis* (Group 3) from neighboring Mohéli, although here the loculi are united basally into a U-shape, and the gynoecious flower differs in being closed in bud. The similarities in androecious floral and staminal morphology of *T. paradoxa*, *T. kirkii*, and *T. moheliensis* may be a result of convergence to accommodate similar pollinators, as the very different gynoecious flower of the latter suggests a closer affinity to the Madagascan *T. capuronii* (also Group 3).

Vernacular name. M'Bweza (Anjouan, fide *Benson 142*, BM).

19. ***Tambourissa moheliensis*** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 300, pl. 2, figs. 9–11. 1982. TYPE: Comore Archipelago. Mohéli: mountains between Fomboni and Drodoni, low montane forest, 500–700 m, 6 Dec. 1967 (fl, fr), *Bernardi 11781* (holotype, Z; isotypes, G, K, P).

Monoecious or subdioecious tree 4–15 m tall by 70 cm diam., the new growth glabrous or with sparse, scattered hairs, the mature leafy stems pale green, terete, 2–5 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles 7–22 mm by 1–1.5 mm; lamina subcoriaceous, ovate, broadly to narrowly elliptic, oblong or rarely obovate, 45–220 mm by 30–70 mm, the apex acute to acuminate, rarely rounded, the base acute to obtuse, cuneate or decurrent, rarely obtuse or rounded, the secondary veins 4–8 pairs, making a 45–65° angle with the costa, the venation visible to 2(–3°) adaxially and to 3(–4°) abaxially, the margin slightly revolute. Gynoecious inflorescence a finely pubescent, cauliflorous pleiochasium or thyrses of up to 20 flowers; androecious inflorescence a ramiflorous plei-

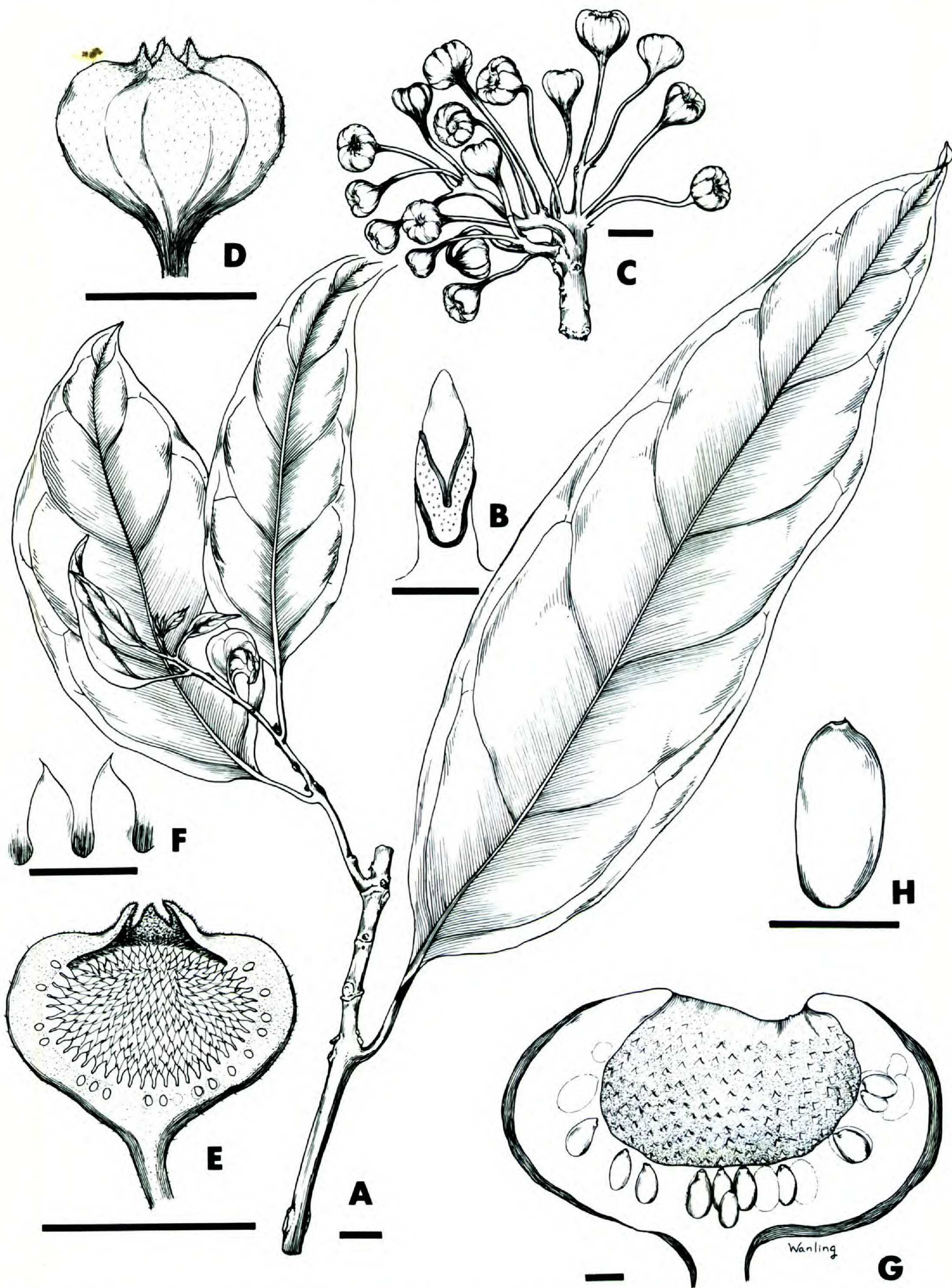


FIGURE 36. *Tambourissa moheliensis* Lorence.—A. Habit.—B. Stamen, adaxial view.—C. Submature gynoecious inflorescence.—D. Gynoecious flower at anthesis, lateral view.—E. Gynoecious flower, longitudinal section.—F. Styles, lateral view.—G. Submature fruiting receptacle, longitudinal section.—H. Fruiting carpel, lateral view. A–E. *Bernardi* 11781 (G). F. *Bernardi* 11759 (G). G, H. *Bernardi* 11781 (Z). Bars equal 10 mm in A, C–E, G, H, and 1 mm in B, F.

ochasium of ca. 5 flowers on the leafless nodes, or the flowers solitary and axillary or rarely subterminal on short leafy shoots; floral axis 15–70 mm by 1–5 mm, finely pubescent or with scattered simple and fasciculate hairs, subtended by several ciliate-velutinous deltoid bracteoles. Androecious flower in bud globose, 4.5–6 mm diam., apiculate with 4 minute, decussate velutinous tepals, the pedicel 10–12 mm by 0.8 mm, bearing scattered hairs, subtended by a minute, deltoid caducous bracteole; at (complete?) anthesis globose, 5–6 mm diam., splitting into 4 shallow, inflexed lobes, each with 3–4 obtuse, scale-like tepals apically on the internal surface, these intergrading with the stamens, the internal receptacle surface glabrous; stamens ca. 50, narrowly acute to subulate, 2–2.5 mm long by 0.6–0.8 mm wide basally, the loculi subparallel, occupying ca. $\frac{2}{3}$ total length of stamen, usually united basally into a single, U-shaped loculus, rarely free, the filament short, broad, the connective acute, prolonged. Gynoecious flower in bud napiform-depressed, pubescent, apiculate with 4 velutinous deltoid tepals 0.5 mm wide, the pedicels 20–40 mm by 1.5–2 mm, pubescent; at anthesis napiform-depressed, 12–16 mm diam. by 7–10 mm long, the orifice X-shaped, 1–2 mm wide, opening by 4 straight to suberect deltoid lobes, these finely pubescent-velutinous on both surfaces; styles numerous, ca. 100–200, conical, slightly ventricose medially, 1–1.3 mm long by 0.3–0.5 mm wide basally, glabrous, the internal receptacle surface velutinous with dense, simple and fasciculate hairs between the styles. Fruiting receptacle borne on the trunk, patelliform to napiform or subglobose, depressed, ca. 120 mm diam. by 70–75 mm long, the internal surface uniformly pale, corky gray-brown, the orifice comprising ca. $\frac{1}{2}$ total width of receptacle, subentire, bearing remnants of the black, deltoid lobes, the walls ca. 20–26 mm thick, the internal surface bearing numerous scattered, narrowly conical, angular styles 1–1.5 mm long by 0.8–1 mm wide basally, interspersed with scattered to dense, simple and fasciculate hairs. Mature carpels ellipsoid to ovoid, compressed, 12–15 mm long, 6–7 mm wide, 4–5 mm thick, the endocarp dark brown, the surface scrobiculate. Figure 36.

Distribution. Endemic to Mohéli, Comores (Fig. 35).

Habitat. The species occurs in montane evergreen forest from ca. 500 to 700 m. Both flowers and fruits are produced in December.

MOHÉLI. FOMBONI: Bamboa, forest, 8 Mar. 1957 (fl), *Anon. in SF-16731* (P). MT. ST. ANTONIO: 600–700 m, in montane and submontane forest, 5 Dec. 1967 (fl, fr), *Bernardi 11759* (G, K, P, Z).

Mohéli, smallest of the four Comores, is probably also the most poorly explored botanically, with only three collections of *Tambourissa* known from the island. After much deliberation I have decided to treat all as a single species, although more extensive collections and field observations are required to ascertain whether or not they are truly conspecific.

The first collection, *Bernardi 11781*, possesses two gynoecious inflorescences with numerous flowers and a single submature fruit. Because it has numerous flowers in both thyrses and pleiochasia in addition to the fruit, I selected it as the type. *Anon. in SF-16731*, from the same locality, corresponds well with the type vegetatively, but the buds are unfortunately immature.

The third collection from Mohéli, *Bernardi 11759*, differs in having nearly glabrous new growth, smaller and more shortly acute or apically rounded leaves with fewer secondary veins oriented at a greater angle to the costa, and stronger, more distinct secondary vein arches. The more sparsely pubescent androecious flowers are in short, ramiflorous pleiochasia of up to five flowers, or rarely solitary and axillary or subterminal. Apart from the fact that the anther loculi are basally confluent in *Bernardi 11759* (Fig. 36B), the narrowly acute to subulate stamens with long connectives and closed, globular androecious flowers most closely resemble those of *T. kirkii* and *T. paradoxa* from nearby Anjouan, except that they contain dark tanniferous idiospores. In terms of androecious floral and staminal morphology, *Bernardi 11759* could represent an undescribed species. The specimen at Geneva, however, has a single corky brown immature fruit with the orifice bearing six deltoid lobes that corresponds well with *Bernardi 11781*, and for this reason I tentatively consider them conspecific.

On the basis of androecious floral and staminal morphology, *Tambourissa moheliensis*, *T. kirkii*, and *T. paradoxa* would appear to be derived from a common ancestor. However, unlike the female receptacles of *T. kirkii*, *T. comorensis*, and *T. leptophylla* (all Group 2), which all have a circular, entire orifice open even in bud, that of *T. moheliensis* is closed in bud and splits open by four, deltoid segments as in *T. capuronii* (Madagascar). Moreover, the floral ground tissue

of both the latter species contains numerous dark brown tanniferous idioblasts not found in the other Comorean species. These characters suggest that *T. moheliensis* was derived from a different ancestor than the other Comorean species and appears most closely allied to *T. capuronii* with which I have placed it in species Group 3.

Vernacular name. Diarou.

20. ***Tambourissa capuronii*** Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957; Cavaco in Humbert, Fl. Madagascar 80: 20, fig. VI:5–8. 1959. TYPE: Madagascar. Diego Suarez: Betsomanga Massif, valley on the S flank, ca. 550 m, 17 Nov. 1950 (fl), *Capuron* 820-SF (holotype, P; isotype, P).

Large monoecious tree 25–30 m tall and 40–60 cm D.B.H., the new growth hirtellous, the mature leafy stems glabrous, petiolate; petioles 12–30 mm by 1.2–1.5 mm; lamina chartaceous to subcoriaceous, abaxially hirtellous to glabrate, elliptic to oblong or obovate, (68–)90–165 mm by 30–74 mm, the apex shortly acuminate, acute or rarely obtuse, the base cuneate to acute, rarely obtuse, the secondary veins 7–10 pairs, making a 55–65° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin moderately revolute. Inflorescence a cauliflorous, unisexual or sexually mixed pleiochasium of 4–15 flowers, or rarely a fascicle of 2–3 flowers, all parts corky brown externally, the floral axis 10–170 mm by 1–5 mm. Androecious flower in bud globose, 15–19 mm diam., corky brown, slightly apiculate with coalescent tepals, the pedicel 28–55 mm by 2–2.5 mm; at anthesis deeply 4(–5)-fid, 40–55 mm diam., the lobes spreading flat; stamens numerous, ca. 300, lanceolate, 6–8 mm long by 1–1.5 mm wide basally, subsessile, the loculi narrow, separate, lateral, occupying the basal $\frac{3}{4}$ – $\frac{4}{5}$ of stamen, the filament short or lacking, the connective acuminate, slightly prolonged, comprising apical $\frac{1}{4}$ – $\frac{1}{5}$ of stamen, the apex sometimes bearing up to 5 simple hairs, the internal receptacle surface glabrous or with scattered simple hairs. Gynoecious flower in bud napiform-depressed, corky brown, 15–20 mm diam.; at anthesis to 35 mm long by 40 mm wide, the apex splitting into ca. 6 thick, irregularly deltoid lobes; styles numerous, ca. 200–300, narrowly conical, slender, 4–5 mm long by 0.5 mm wide basally, solitary or coalescent into groups of up to 12, the internal receptacle surface densely pilose between the styles and around the ori-

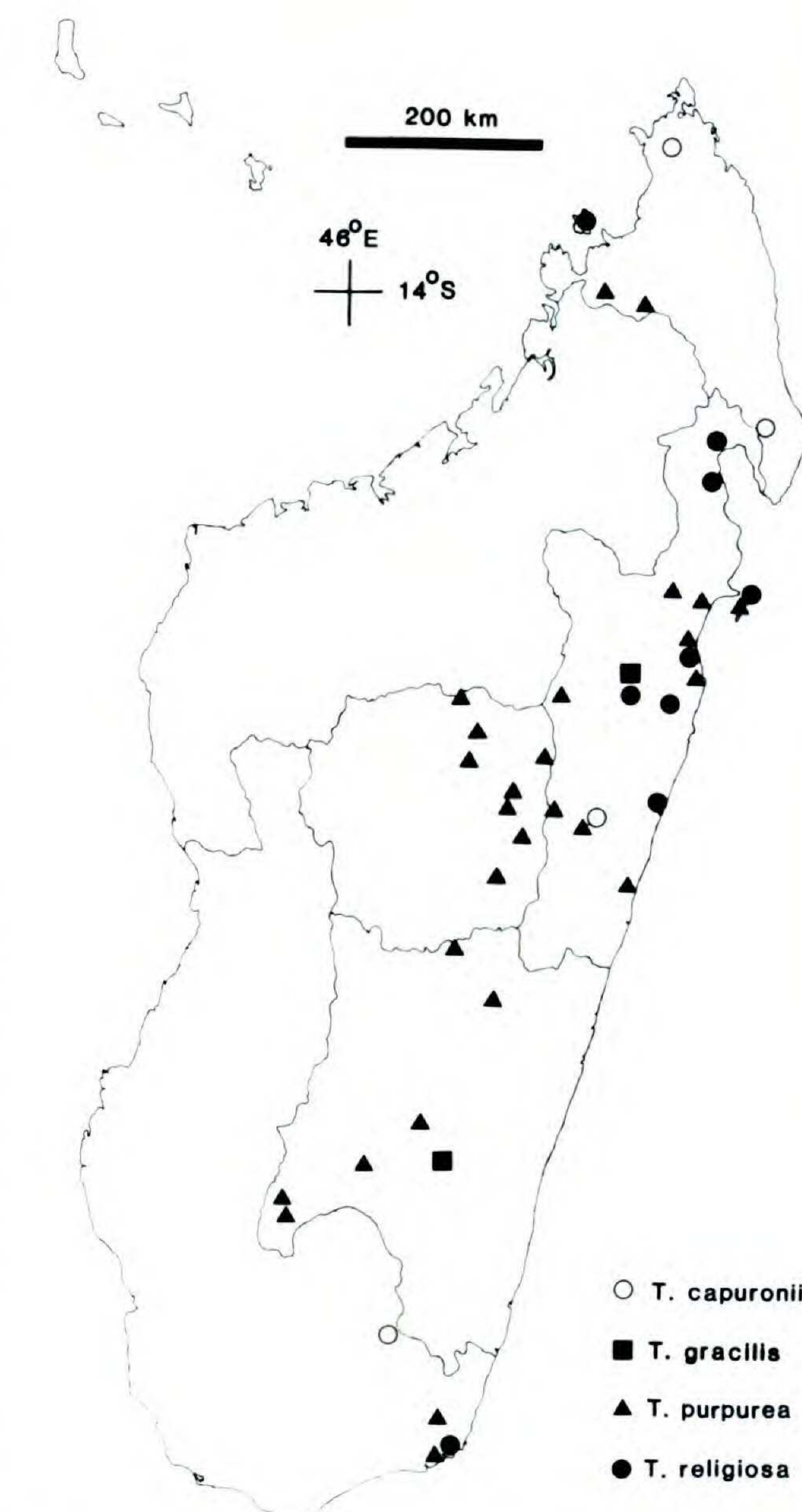


FIGURE 37. Distribution map of some *Tambourissa* species in Madagascar.

fice; pedicel to 75 mm by 5 mm. Submature fruiting receptacle cupuliform, externally corky, 35 mm long by 55 mm diam., the carpels ovoid-compressed, to 13 mm by 8 mm.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. Contrary to Cavaco's original (1957d) statement that the species was a highly restricted endemic, his subsequent list of exsiccata (1959) shows *Tambourissa capuronii* to be fairly widely distributed both in lowland Myristicaceae/*Anthostema* wet forest from ca. 300 to 800 m, and also in *Tambourissa*/*Weinmannia* montane wet forest from ca. 800 to 1,400 m, ranging from Mt. D'Ambre (Diego Suarez) in the north, south along the eastern escarpment, to the Mandrare River near Fort Dauphin in the southeast. The species was said by Capuron to be very abundant in 1950 at Betsomanga between 350

and 600 m. A canopy tree reaching ca. 30 m, it flowers in November–December and is one of the largest members of the genus.

MADAGASCAR. DIEGO SUAREZ: forêt d'Ambre, 1,200 m, Sept. 1926 (fl), *Perrier de la Bâthie* 11741 (P). TAMATAVE: Analamazaotra forest (Perinet) 800 m (fl), *Perrier de la Bâthie* 10087 (P); *Perrier de la Bâthie* 10095 (P); Antasibe, Soanierana, E coast, 350 m, 10 Dec. 1938 (fl), *Lam & Meeuse* 5835A (P). TULEAR: upper basin of the Mandrare River (SE), pass and summit of Marosoui, forest on gneissic laterite, 1,000–1,400 m, 14–15 Nov. 1928 (fl), *Humbert* 6606 (B, G, 2 sheets; K, MAD, P).

Tambourissa capuronii appears to be most closely related to the Comorean *T. moheliensis* with which it comprises species Group 3. The latter is distinguishable by its much smaller Androecious flowers and stamens, and styles which are never coalescent into groups as in *T. capuronii*. None of the other Madagascan species appears to be closely allied to *T. capuronii*.

21. *Tambourissa religiosa* (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, *Pflanzenr.* 4, 101: 71. 1901; Drake in Grandidier, *Hist. Phys. Madagascar* 1(1): 23. 1902; Perk., *Pflanzenr.* 4, 101 (Nachtr.): 44. 1911; Cavaco in Humbert, *Fl. Madagascar* 80: 36. 1959, excluding fig. X:5 (which is *T. elliptica* subsp. *micrantha*). *Ambora religiosa* Tul., *Ann. Sci. Nat. (Paris)* 4(3): 30. 1855; Tul., *Monogr. Monim.* 30, pl. XXVII. 1855. TYPE: "Bourbon" (Réunion). (Fide Richard, but probably Madagascar), ca. 1851 (fl), *Boivin s.n.* (lectotype, P, here designated).

Ambora tambourissa Boiv. ex Tul., *Monogr. Monim.* 303. 1855, non Lam. ex Steud.

Tambourissa boivinii A. DC., *Prodr.* 16(2): 659. 1868; Perk. & Gilg, *Pflanzenr.* 4, 101: 70. 1901; Drake in Grandidier, *Hist. Phys. Madagascar* 1(1): 23. 1902; Perk., *Pflanzenr.* 4, 101 (Nachtr.): 42. 1911. TYPE: Madagascar. Tamatave: Sainte Marie Island, Lafondroa forest, Mar. 1847 (fr), *Boivin* 1728 (holotype, P).

Tambourissa quadrifida sensu Drake in Grandidier, *Hist. Phys. Madagascar* 1(1): 21. 1902, pro parte (as to *Baron* 2504), non Sonnerat.

Monoecious shrub, treelet, or small tree 4–5 m tall, the new growth glabrous, the mature leafy stems ascendant, dark brown to stramineate, 2.5–6 mm diam. Leaves opposite to subopposite, glabrous, petiolate; petioles (10–)15–30 mm by (1–)1.5–2.5 mm; lamina subcoriaceous to coriaceous, ovate elliptic, elliptic, oblong, narrowly oblong or obovate, 70–150(–175) mm by (16–)30–

60 mm, the apex shortly acuminate, bluntly acute, obtuse or retuse, the base acute, cuneate or obtuse, often $\pm$ decurrent, the secondary veins 6–10 pairs, making a 60–70° angle with the costa, the venation obscure or visible to 2–3° adaxially, visible to 3–4° abaxially, the intramarginal loops uniting to form a conspicuous, partial marginal fimbrial vein, the margin thickened, moderately to strongly revolute. Inflorescence glabrous, either a terminal, axillary, or ramiflorous dichasium of 3 flowers or condensed pleiochasium of 5–7 flowers (the gynoeceous flower terminal, if present), or the flowers solitary and terminal or axillary, the floral axis 1–7 mm by 1.5–2 mm, the axis and pedicels subtended by several glabrous to sparsely ciliate, broadly deltoid bracteoles with pale margins. Androecious flower in bud blackish to yellowish, globose to napiform, 7–10 mm diam. by 4–6 mm long, $\pm$ depressed, apiculate with 2–4 minute, deltoid glabrous tepals, the pedicel 3.5–5 mm by 1–1.5 mm; at anthesis unknown, presumably splitting into 4 shallow lobes (as in *T. purpurea*); stamens in bud ca. 60–82, linear-ellipsoid to slightly ovoid, 0.8–1 mm long by 0.5–0.7 mm wide, the filament short, distinct, slender, the loculi lateral, separate (rarely confluent apically), the connective rarely prolonged into an apicule, the internal surface with sparse hairs. Gynoeceous flower in bud napiform-depressed, the pedicel 6–7 mm by 1–1.5 mm; at anthesis 8–11 mm diam. by 5–7 mm long, the orifice shallowly 4-lobed, X-shaped, 0.5–1.5 mm wide, the walls thick; styles numerous, ca. 300, conical, acuminate, slightly ventricose, 0.5–1.7 mm long by 0.3–1.5 mm wide basally, the internal receptacle surface with clusters of simple hairs between the styles. Fruiting receptacle terminal, solitary, or rarely paired, napiform-depressed to subglobose, to 52 mm diam. by 40 mm long, the external surface smooth, dark brown with corky patches, the orifice ca. 12 mm diam., comprising $\frac{1}{4}$ – $\frac{1}{5}$ total width of receptacle, subcircular, subentire, the walls 10–17 mm thick, the internal surface with scattered conical-columnar styles 0.3–0.5 mm long and wide basally, interspersed with scattered hairs. Mature (?) carpels ovoid-compressed, 7–9 mm long, 5–6 mm wide, 4–5 mm thick, the endocarp light brown to beige, the surface shallowly scrobiculate.

Distribution. The species is endemic to Madagascar. Cordemoy (1895) erroneously cites the species as occurring in Réunion, but was actually referring to *Tambourissa crassa* (q.v.). The lec-

otype of *T. religiosa* was said by Richard to have come from Bourbon (Réunion), but this is undoubtedly due to a mixup in herbarium labels, because his other collections of the species are all from Madagascar and no other authentic specimens are known from Réunion (Fig. 37). It was selected because it represents the best of the four syntypes. The type of *T. boivinii*, although in poor condition, is clearly referable to *T. religiosa*.

Habitat. In Madagascar *Tambourissa religiosa* appears to be commonest in the eastern littoral forests where it occurs sympatrically with *T. purpurea*. The species ranges inland to the mountainous central plateau from altitudes of 1,500 to 1,700 m, and across the northwestern region to the offshore island of Nosy Be.

MADAGASCAR. DIEGO SUAREZ: Nossi Be, 23 July 1840 (st), *Pervillé* 295 (P, syntype); 10 Oct. 1840 (fr), *Pervillé* 328 (P, syntype). TAMATAVE: Ambila, 1 May 1928 (fl), *Decary* 6288 (MAD, P); 10 May 1928 (fl, fr), *Decary* 6554 (K, MAD, P); Rantabe, N of Tamatave, littoral forest, 1 June 1969 (st), *Guillaumet* 3002 bis (MAD); Maroa, forests within Antongil Bay, 1867 (fl), *Moqueries* 66 (G, Z); Reserve no. 1, Tamatave, 21 June 1950 (fl), *Rakotoniana sub RN* 3956 (MAD, 2 sheets); Sainte Marie Island (East Coast), Sept. 1851 (fl), *Boivin s.n.* (P, syntype); (fl), *Boivin s.n.* (P, syntype); Mar. 1847 (fr), *Boivin* 1728 (P, holotype of *T. boivinii*); Ambila, Lemaitsoa, littoral forest, Aug. 1975 (fl, fr), *Rakotozafy* 1293 (MAD); AndronDRAMANIKa, Rahobevava, 830 m (near Lac Alaoatra), 10 May 1951 (fr), *Cours sub Herb. Alaotra* 4270 (MAD). WITHOUT PRECISE LOCALITY: Central Madagascar, 1883 (fl), *Baron* 2499 (K); (fl), *Baron* 2504 (K); Dec. 1883 (fl), *Baron* 2766 (K, 2 sheets); East Coast, Mar. 1891 (fr), *Baron* 6043 (K); 1865 (fl), *Gerrard* 35 (K); 1883 (fl), *Humbolt* 190 (K).

Tambourissa religiosa belongs to species Group 4 and appears to be most closely allied to *T. purpurea*, another Madagascan species with structurally similar leaves and flowers. Observations on living material of *T. religiosa*, however, are required to ascertain whether or not its gynoeceous flowers produce a mucilaginous "hyperstigma" as do those of *T. purpurea* (studied by Endress, 1979 and 1980b, as *T. religiosa*). Ripe fruiting receptacles of both species are smooth and reddish as opposed to those of most congeners which are pale brown and corky.

Tambourissa religiosa is distinguishable from *T. purpurea* by its floral receptacles which are more than twice as large, its more numerous stamens with separate loculi and distinct filaments, its more numerous, acute styles, and by its larger, more coriaceous leaves with a thicker hypodermis, prominent partial marginal fimbrial vein, and revolute margins.

Vernacular names. Ambora, Laingafora (Madagascar). According to Commerson, certain Malagasy tribes used *Tambourissa religiosa* in a religious context, burying their dead with its branches.

22. *Tambourissa purpurea* (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 69, fig. 18:5. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 39, fig. V:1. 1959. *Ambora purpurea* Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 301, pl. XXVI. 1855. TYPE: Madagascar. Tamatave: Sainte Marie Island (ca. 1850) (fl, fr), *Bernier* 262 (lectotype, P, here designated; isoelectotype, P).

Tambourissa rota Baker, J. Linn. Soc., Bot. 20(128): 240. 1883; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Perk., Gatt. Monim. fig. 34:5. 1925; Cavaco in Humbert, Fl. Madagascar 80: 38, fig. X:6. 1959. TYPE: Madagascar. Central Madagascar: without precise locality (ca. 1881) (fl, fr), *Baron* 764 (lectotype, K, here designated; isoelectotype, P).

T. quadrifida sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, non Sonn.

T. rota var. *longipetiolata* Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911. TYPE: Madagascar. Central Madagascar: without precise locality (fr), *Baron* 1642 (holotype, K).

Monoecious shrub, treelet, or small tree attaining 10 m tall and 30–40 cm D.B.H., the bark gray-black, longitudinally fissured, the branches often decumbent and trailing, the new growth glabrous or with rare, scattered hairs, the mature leafy stems brownish, 2–3 mm diam., terete. Leaves opposite to subopposite, rarely ternate on vigorous sucker shoots, glabrous, petiolate; petioles 3–10(–17) mm by 0.8–1.3 mm, red to purple when living; lamina chartaceous to subcoriaceous, ovate-elliptic, elliptic, oblong, narrowly oblong or obovate, (25–)40–85(–100) mm by (10–)15–40(–44) mm, the apex acuminate, acute, obtuse or retuse, the base cuneate, acute, obtuse, truncate or even subcordate, often $\pm$ decurrent, the secondary veins 4–11 pairs, making a 60–70° angle with the costa, the venation visible to 2–4° or obscure adaxially, visible to 2–3° abaxially, the margin plane to slightly revolute. Inflorescence ramiflorous, axillary, or terminal on leafy shoots, a 3-flowered dichasium or a contracted pleiochasium of 5 flowers (the gynoeceous flower terminal, if present), or the flowers solitary, or in sparse fascicles on old stems, the floral axis

1–4 mm by 1 mm, glabrous to puberulent, the axis and pedicels subtended by 1 to several ciliate to hirsute, naviculate bracteoles. Androecious flower in bud sparsely pubescent to glabrous, globose-depressed to napiform-depressed, 2–3(–4) mm diam. by 2.5–3.5(–4) mm long, the apex with 1–3 pairs of minute, acute to rounded ciliate tepals, the pedicel 2.5–6(–10) mm by 0.6–1 mm; at anthesis 2.5–3.5 mm diam., shallowly (3–)4-fid for up to $\frac{1}{2}$ its length, the lobes incurved or spreading slightly, the orifice 1–3 mm diam.; stamens 20–32, acutely deltoid to obtusely deltoid, 0.7–1.2 mm long by 0.6–1 mm wide, the loculi confluent apically into a single, crescentiform loculus, the filament very short or sessile, the internal receptacle surface glabrous or with rare, scattered hairs. Gynoecious flower in bud globose-depressed to napiform-depressed, glabrous to sparsely pubescent, apiculate with 2–3 pairs of minute tepals, the pedicel 5–6 mm by 1 mm; at anthesis urceolate-globose to urceolate-napiform, 4(–7) mm diam. by 4(–7) mm long, the orifice 3–4-lobed, 0.5–1 mm diam., when living occluded by a mucilaginous plug, the inner tepals stigmatic; styles 35–70(–90), shortly columnar, apiculate, 0.3–0.4 mm long by 0.2–0.3 mm diam., the internal receptacle surface glabrous or with rare, scattered hairs between the styles. Fruiting receptacle terminal, solitary, globose-urceolate, $\pm$ depressed, 28–50 mm diam. by 25–40 mm long, the external surface dark reddish brown to blackish, occasionally mottled with pale gray-brown, corky patches, the orifice subentire, $\pm$ circular, 2–7 mm diam., comprising $\frac{1}{10}$ – $\frac{1}{6}$ total width of the receptacle, the walls 8–11 mm thick, the internal surface with scattered, subcircular styles ca. 0.5 mm diam., glabrous or with rare, scattered hairs. Mature carpels ovoid-compressed, 6–9 mm long, 4–7 mm wide, 3.5–5 mm thick, the endocarp brown, the surface scrobiculate to reticulate-foveate. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. *Tambourissa purpurea* is one of the most widely distributed members of the genus in Madagascar, along with *T. hildebrandtii* and *T. religiosa*. Quite variable vegetatively, it displays a wide ecological amplitude ranging from littoral forest along the east coast, through the lowland and submontane wet forest zones of the eastern escarpment (up to ca. 1,400 m), and into montane forest of the central plateau (ca. 1,400–

1,600 m). It also extends westward into the semi-deciduous dry forest zone of the western sector as far as the Isalo massif, where it is apparently able to survive annual burning, taking on a shrubby habit with numerous erect coppice shoots.

In living plants, floral receptacles of *Tambourissa purpurea* range from green to dark reddish purple. The gynoecious flowers produce a mucilaginous plug or “hyperstigma” (see Endress, 1979, 1980b) that is probably functional in pollination. Androecious flowers of *Lorence 1725* (MO) produced a faint sweet, almost musky, odor.

MADAGASCAR. FIANARANTSOA: Isalo, 13 Apr. 1961 (fl), *Anon. sub Herb. Peltier 3044* (MAD); Ihosy, Mont Lalandro, 1,100–1,200 m, 5 Nov. 1967 (fr), *Bernardi 11230* (K); Route no. 7, 39 km N of Ambositra, 1,250–1,350 m, 24 Jan. 1975 (fr), *Croat 29458* (MAD, MO); 10 km W of Ivato on Route 35, 1,365 m, 25 Jan. 1975 (fr), *Croat 29545* (MAD, MO); Massif d’Isalo, 10 km W of Ranohira, Route 7, 810 m, 3 Feb. 1975 (fl), *Croat 30568* (MAD, MO); Ambohimombo forest (Fanala), 1,350–1,440 m, 4 Jan. 1895 (fl), *Forsyth Major 328* (K); (fl), *Forsyth Major 340* (K); 21 Jan. 1895 (fr), *Forsyth Major 710* (K); Betsileo Land, 1880 (fr), *Langley Kitching s.n.* (K); National Route no. 7 at 11 km W of Ambalavao, 950 m, 5 Nov. 1978 (fl), *Lorence 2042b* (K, MAD, MAU, MO, P, Z); (fl), *Lorence 2044* (K, MAD, MO, Z); National Route no. 7 at 9 km SW of Ranohira (Isalo), 800 m, 6 Nov. 1978 (fr), *Lorence 2058* (MAD, MO); (fr), *Lorence 2059* (MAD, MO); (st), *Lorence 2060* (MAD, MO). MAJUNGA: Natural Reserve no. 4, Marovato, Ambanja, 10 July 1952 (fr), *Safy sub RN 4180* (MAD, 2 sheets). TAMATAVE: Soanierana, Ivongo (near Sainte Marie Island), 27 Dec. 1949 (fr), *Anon. sub SF 2346* (MAD); Anjahana, Foule Pointe, 12 June 1950 (fr), *Anon. sub SF 2585* (MAD); Natural Reserve no. 3, Sahatavy, Fenoarive, 17 June 1952 (fl), *Anon. sub RN 4137* (MAD); Vohimaranitra, Tamatave, 26 Jan. 1951 (fr), *Anon. sub RN 1989* (MAD); Sainte Marie Island, Tafondron Forest, Mar. 1847 (fl, fr), *Boivin 1729* (P, syntype, 2 sheets); Morarano, pseudosteppes on dry slopes (W of Lac Alaotra), Dec. 1954 (fl), *Bosser 7502* (MAD); on sand between Mahanoro and Vatomandry, 2 July 1972 (fr), *Cremers 2310* (MAD, 2 sheets); Ambila, littoral forest, 8 May 1928 (fr), *Decary 6450* (P); Fenoarivo, 18 Mar. 1930 (fl), *Decary 7633* (MAD); National Route no. 2 at 89 km E of Tananarive, Mandraka Forest, 1,400 m, 30 Oct. 1978 (st), *Lorence 2036* (MAD, MO); Perinet, 70 km E of Tananarive (cultivated in Heidelberg Bot. Garden) Oct. 1976 (fl), *Rauh M 138* (Z). TANANARIVE: Analabe, Anjozorobe, Mar. 1953 (fr), *Bosser 5219* (MAD, 2 sheets); Tampoketsa, Ankazobe, Pk 120, road to Majunga, Apr. 1955 (fr), *Bosser 7855* (MAD); Andramasina, Ambatolampy (fl, fr), *Bosser 12466* (MAD, 2 sheets); forest at Pk 142 along the road from Tananarive to Majunga, 8 July 1971 (fr), *Cremers 1641* (MAD); Tananarive, Tsimbazaza Park, 1,200 m, 17 Jan. 1975

(fl), *Croat* 28636 (MAD, MO); near Tananarive, 28 July 1928 (fr), *Decary* 6610 (MAD); Tananarive, Tsimbazaza Park, cultivated in back of Philippe Morat's house (originally from Perinet), 28 May 1974, *Gentry & Morat* 11964 (MAD, MO); forests of Tampoketsa, May 1956 (fr), *Rialinansy* 1027 (MAD); bottom of the valley Ambohimanga south, 9 Nov. 1963 (st), *Rakotozafy* 204 (MAD); "tapias" (*Uapaca* forest), Pk 36, road to Antsirabe, 16 Feb. 1966 (fl), *Rakotozafy* 460 (MAD); Vakinankaratra, Ambatolampy, banks of the Onive River, near Tsinoarivo, 1,600 m, 1 Dec. 1912 (fr), *Viguiet & Humbert* 1913 (G). TULEAR: along road through mountain forest in Chaines Anosyennes from Fort Dauphin to Ranamafona, 40–60 m, 1–28 km from Route no. 10, 19 Feb. 1975 (fr), *Croat* 31778 (MAD, MO); (fr), *Croat* 31779 (MAD, MO); dunes, Fort Dauphin (fr), *Pernet sub Herb. Inst. Sci. Madagascar* 29 (MAD); Fort Dauphin (fl), *Rauh* 1440 (MAD). PROVINCE UNCERTAIN: Amtranokofa, Natural Reserve, 8 July 1950 (fr), *Anon. sub SF* 43 (MAD); forest N of the road to Nickaville, 29 Dec. 1944 (st), *Anon. sub Herb. Alaotra* 2081 (MAD); Antsahabe to Antsakalalina, 20–40 m, 5 Apr. 1949 (fr), *Anon. sub Herb. Alaotra* 3607 (MAD); Andrangomalaka, Central Madagascar, 1881 (fr), *Baron s.n.* (K); 1882 (fl), *Baron* 1239 (K, syntype of *T. rota*); (st), *Parker s.n.* (K); Central Majakotompo, Nov. 1955 (fr), *Bosser* 8709 (MAD); Antongona, rocks, Jan. 1960 (fl), *Bosser* 13509 (MAD); Pk 44, road to Majunga, Mar. 1963 (fr), *Bosser* 17192 (MAD); valley of the Saonjo, May 1964 (fr), *Morat* 1140 (MAD); Antongona, 16 Jan. 1960 (fl), *Peltier* 1763 (MAD); Maroamalona, Rankafina, 14 Nov. 1963 (fr), *Rakotozafy* 228 (MAD); Tsaravinany, Apr. 1966 (fr), *Rakotozafy* 588 (MAD). WITHOUT PRECISE LOCALITY: 1881 (fl, fr), *Baron* 790 (K, P, syntypes of *T. rota*); 1882 (fl), *Baron* 1361 (K, P, syntypes of *T. rota*); (fr), *Baron* 2996 (K); 1883 (fr), *Baron* 3024 (K, P); 1885 (fr), *Baron* 3515 (K, P); (st), *Baron* 3575 (BM); (fr), *Baron* 4241 (K, P); (fr), *Baron* 4325 (K); 1892 (st), *Baron* 6675 (BM); (st), *Parker s.n.* (K); North Madagascar, 1892 (fr), *Baron* 6439 (K). CULTIVATED: Missouri Botanical Garden, grown from wild seed obtained from Madagascar, 23 June 1977 (fl), *Lorence* 1725 (MO); (fl), *Lorence* 1726 (MO); 13 Feb. 1980 (fl), *Lorence* 2954 (MO).

Although *Tambourissa purpurea* is extremely variable in terms of foliar morphology, even on a single individual (e.g., *Croat* 29458, MO), its flowers are quite constant and the smallest in the genus. Along with *T. gracilis* and *T. religiosa*, it belongs to species Group 4. Flowers of *T. religiosa*, however, are about twice as large as those of *T. purpurea*, have more numerous parts, and the leaves are thicker with a well-developed hypodermis of (3–)5–6 cell layers comprising ca. $\frac{1}{3}$ – $\frac{1}{2}$ of the total laminar thickness. That of *T. purpurea* is only (1–)2–3 cell layers thick and comprises only $\frac{1}{6}$ – $\frac{1}{3}$ of the total laminar thickness. Also, *T. purpurea* lacks the prominent partial marginal fimbrial vein of the former species. Both occur sympatrically in eastern and central

Madagascar and no hybrids or intermediates are known to occur.

Tambourissa purpurea is perhaps even more closely allied to *T. gracilis* in terms of foliar and androecious floral morphology (gynoecious flowers are unknown in the latter). The pleiochasia are much laxer in *T. gracilis*, however, with a much longer floral axis and pedicels.

Vernacular names. Ambora, Ambora vavy, Rota, Villainque-possa (Madagascar).

23. *Tambourissa gracilis* Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911; Cavaco in Humbert, Fl. Madagascar 80: 35. 1959. TYPE: "Central Madagascar." Without precise locality (probably Tananarive or Fianarantsoa): ca. 1888 (fl), *Baron* 2885 (holotype, K; isotype, P).

T. leptophylla sensu Drake in Grandidier, Hist. Phys. Madagascar 1(1): 23. 1902 non (Tul.) A.DC.

Dioecious (?) treelet or small tree 8–10 m, the mature leafy stems glabrous, 1.5–2.5 mm diam. Leaves opposite, glabrous, petiolate; petioles 14–17 mm by 1 mm; lamina chartaceous, elliptic or rarely oblong, 75–120 mm by 26–45 mm, the apex long acuminate, the base acutely cuneate, decurrent, the secondary veins 6–9 pairs, making a 65–85° angle with the costa, the venation raised and visible to 4° on both surfaces, the margin plane to slightly revolute. Androecious inflorescence ramiflorous on leafless nodes or axillary, a unisexual pleiochasium of 3–7 flowers, sparsely pubescent with pale, appressed hairs, the floral axis 7–25 mm by 1 mm, subtended by several basal bracteoles. Androecious flower in bud globose, 6–8 mm diam., apiculate with a pair of semicircular, obtuse tepals, the pedicel 5–13 mm by 1 mm, subtended by 1(–2) hirsute, naviculate bracteoles 1–2 mm long; at (full?) anthesis globose, 6–8 mm diam., the subcircular orifice 1–2 mm diam., occasionally splitting slightly, flanked internally by several pairs of obtuse, scale-like tepals; stamens ca. 50, broadly deltoid, 1.2–1.7 mm long by 1 mm wide, the loculi occupying almost entire length of the stamen, confluent apically into a single, crescentiform loculus, the filament very short or sessile, the internal receptacle surface with rare, scattered hairs. Gynoecious inflorescence unknown. Submature fruiting receptacles borne in clusters of 2–3, shallowly cupuliform, 30–55 mm wide by 20–30 mm long, the orifice comprising $\frac{2}{3}$ – $\frac{3}{4}$ total width of

fruit, the styles conical, 0.6–0.8 mm long; fruiting carpels ovoid-compressed, 9–10 mm long by 7–8 mm wide, tan.

Distribution. Endemic to Madagascar (Fig. 37).

Habitat. According to Humbert (1965) and Cavaco (1959), *Tambourissa gracilis* occurs in high altitude ericoid heath formation (ca. 1,800–2,700 m) on mountains of the central plateau and vicinity. However, a fruiting specimen (Humbert 3688, P) named by him and cited by Cavaco (1959) is closer to *T. purpurea*, from which it differs in having disorganized venation characteristic of neither species. As the specimen lacks flowers, a more complete analysis is impossible.

MADAGASCAR. DIEGO SUAREZ: Tsaratanana Massif, 1,400 m, Nov. 1912 (fr), *Perrier de la Bâthie* 10105 (P).

Tambourissa gracilis belongs to species Group 4. With respect to its androecious flowers, which have short, subsessile stamens and apically confluent loculi, it appears to be most closely related to *T. purpurea* which differs in having a shorter floral axis and pedicels. Foliar morphology of the two species is virtually identical, also resembling that of *T. madagascariensis* (Group 2A). Further collections of this imperfectly known species, especially gynoeceous flowers and fruits, are needed to better understand its affinities.

24. *Tambourissa pedicellata* Baker, Fl. Mauritius 289. 1877; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Vaughan, Mauritius Inst. Bull. 1(1): 76. 1937. TYPE: Mauritius. Without precise locality; in the shade of humid forests, on the high mountains, 1864 (fl, fr), *Bouton s.n.* (lectotype, K).

Ambora amplifolia sensu Tul., Monogr. Monim. 299. 1855, pro parte, non Boj. ex Tul.

Tambourissa amplifolia sensu A.DC., Prodr. 16(2): 659. 1868, pro parte; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901, pro parte, non (Boj. ex Tul.) A.DC.

Monoecious tree attaining 15 m tall and 30 cm D.B.H., the crown compact, the bark pale brown, smooth, flaking, the new growth sparsely puberulent, glabrescent, the mature leafy stems 2.5–6 mm diam., terete, the nodes dilated. Leaves opposite, rarely subopposite, glabrous, petiolate; petioles (2–)6–13 mm by 1.5–3 mm; lamina chartaceous to coriaceous, elliptic to narrowly elliptic or oblong, rarely broadly elliptic to

suborbiculate, (30–)50–160(–200) mm by (15–)22–80(–120) mm, the apex acuminate, acute, obtuse, rounded or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 5–12 pairs, making a 50–65° angle with the costa, the venation obscure adaxially and visible to 2(–3°), dark brown abaxially and visible to 3(–4°), the margin slightly thickened, moderately revolute. Inflorescence a glabrous, ramiflorous (rarely terminal), leafless or leafy, unisexual or sexually mixed pleiochasium of 5–14 flowers, or a cauliflorous, leafy or leafless pleiochasium or rarely dichasium, the floral axis (15–)35–200 mm by 1.5–4 mm, often $\pm$ flattened, frequently subtended by several deltoid-naviculate puberulent bracteoles; flowers monomorphic. Androecious flower in bud napiform-depressed, 7–11 mm diam. by 4–7 mm long, externally smooth with scattered hairs, the apex with 4 minute, puberulent tepals, the pedicel long, slender, 15–66 mm by 0.7–1.5 mm, subtended by a single puberulent, subulate-deltoid bracteole 1–2 mm long or by a small leaf; at anthesis shallowly 4–6-fid, subglobose, 10–14 mm diam., the lobes thick, short, acuminate, incurved to erect, the orifice comprising $\frac{1}{2}$ – $\frac{2}{3}$ total width of the receptacle; stamens 50–70, minute, deltoid to ellipsoid, 0.6–1 mm long by 0.5–0.8 mm wide, the loculi short, broad, subparallel, separate or occasionally confluent apically, sometimes $\pm$ unilateral, occupying $\frac{2}{3}$ – $\frac{3}{4}$ total length of the stamen, the filament short, basally ventricose, the connective not prolonged, the internal receptacle surface glabrous. Gynoeceous flower in bud subglobose to napiform-depressed, 8–10 mm diam. by 5–7 mm long, externally smooth with scattered hairs, the apex with 3–4 minute, puberulent tepals, the pedicel as in the androecious flower; at anthesis shallowly 4–7-fid, subglobose, 6–12 mm diam. by 5–7 mm long, the lobes thick, acute to acuminate, erect, the orifice subentire, comprising ca. $\frac{1}{2}$ – $\frac{2}{3}$ total width of the receptacle, the walls thick; styles ca. 60–180, conical, 0.8–1.2 mm long by 0.3–0.4 mm wide basally, the apex slightly papillose, the base ventricose, the internal receptacle surface glabrous or with sparse clusters of hairs between the styles. Fruiting receptacle produced on the branches, solitary or in a leafy pleiochasium of up to 5 fruits, $\pm$ subglobose, 18–32 mm diam. by 12–25 mm long, the orifice small, shallow, comprising ca. $\frac{1}{4}$ – $\frac{1}{2}$ total width of the receptacle, the rim subentire, thickened, with persistent deltoid lobes, the external surface mottled, pale corky brown with darker patches,

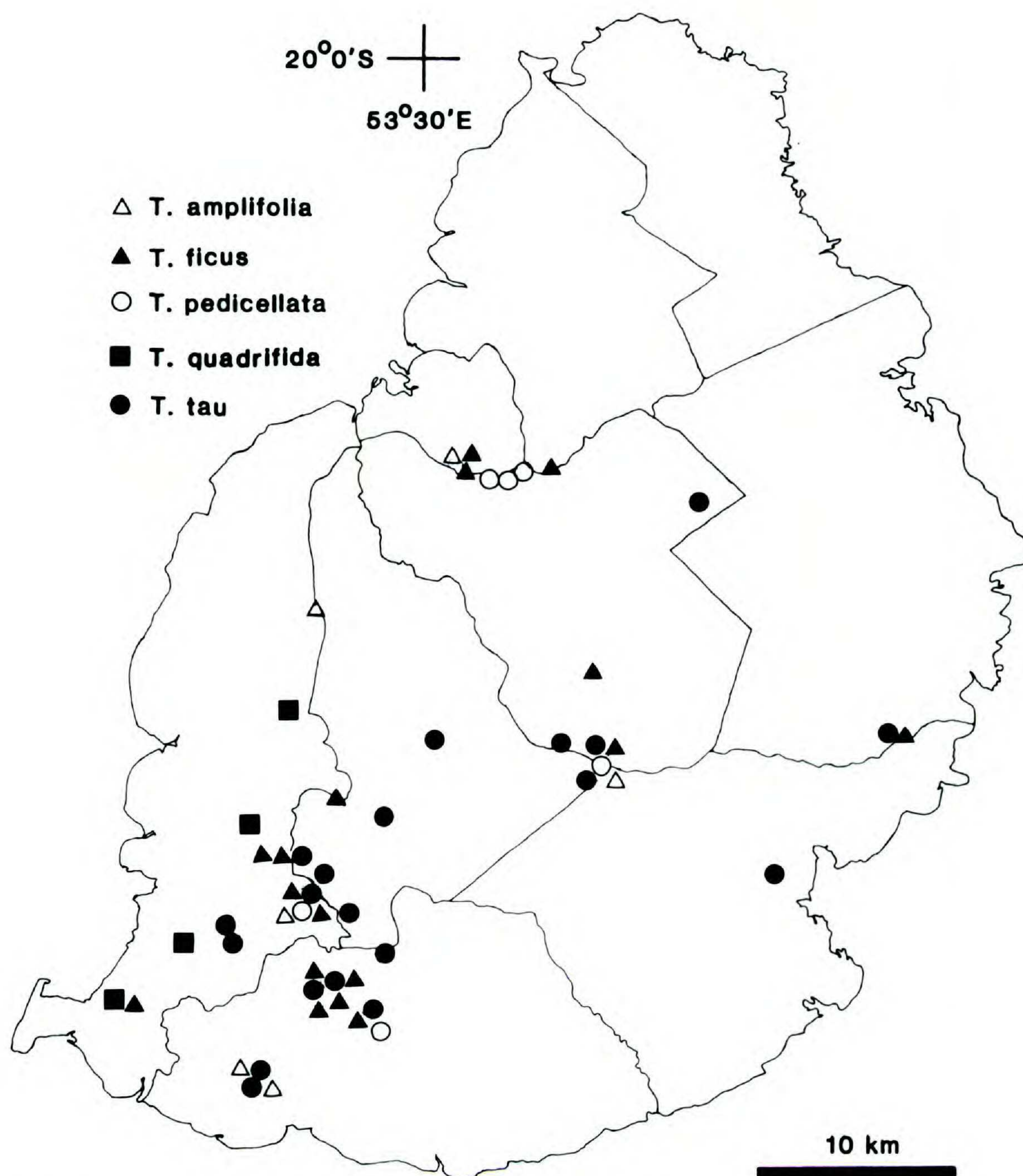


FIGURE 38. Distribution map of some *Tambourissa* species in Mauritius.

the cavity small, the numerous styles conical, 0.6–1 mm long by 0.4–0.7 mm diam. basally, interspersed with rare, scattered hairs, the pedicel slender, 20–55 mm by 1.5–2.5 mm. Mature carpels ovoid-compressed, 8–11 mm long, 6–8 mm wide, 4–6 mm thick, the endocarp dark brown with 1 to several longitudinal, $\pm$ branching ridges, the surface foveate-scrobiculate. Gametic chromosome number, $n = 19$.

Distribution. The species is endemic to Mauritius (Fig. 38).

Habitat. *Tambourissa pedicellata* is presently known only from four localities in wet and cloud forest: the southern flank of the Pieter Both mountain range, where I estimate the total population to consist of 50 to 100 individuals; at Mt.

Lagrange, where a small population occurs in cloud forest near the summit; in Bassin Blanc crater, where a single individual was located. Vaughan and Wiehe (1941) recorded *T. pedicellata* from Macabé forest (*Vaughan 1327 sub MAU 2358, MAU*), but I was unable to relocate it there during extensive searches made in 1974–1977 and again in 1978–1979. In 1983, W. Strahm (pers. comm.) located an “individual” of *T. pedicellata* at Macabé whose trunk was fused with that of *T. sieberi* in what apparently represents a perfect natural graft.

My observations on the Pieter Both population during the course of a year showed the plants to be evergreen and not deciduous as stated by Vaughan and Wiehe (1941). Most individuals

here flowered from February through April 1979, although one tree was flowering in November 1978. Fruits generally ripened in February. Living flowers of *T. pedicellata* produce little apparent odor, although a faint, fruity smell was detected in some. Buds and receptacles are mottled green externally, and the stamens may be cream, yellow, or yellowish pink, whereas the styles range from bright orange to reddish orange.

MAURITIUS. BASSIN BLANC CRATER: wet forest near lake, ca. 500 m, 6 July 1979 (st), *Lorence 2967* (MO). MACABÉ FOREST: Macabé transect (symbol T₂) 16 June 1937 (st), *Vaughan 1327 sub MAU 2358* (MAU). MT. LAGRAVE: S slope facing Eau Bleue reservoir, near summit, ca. 600–628 m, 24 May 1979 (st), *Lorence 2966* (MO). PIETER BOTH MOUNTAIN RANGE: S flank, 500–600 m, 29 Nov. 1978 (fl), *Lorence 1834* (K, MAU, MO, 2 sheets; P); 13 Feb. 1979 (fl), *Lorence 2384* (K, MAU, MO, 2 sheets; Z); (fl, fr), *Lorence 2385* (B, G, K, MAU, MO); (fl, fr), *Lorence 2386* (K, MAU, MO, P, REU); 19 Apr. 1979 (fl), *Lorence 2598* (MAU, MO); (fl), *Lorence 2599* (MAU, MO). QUARTIERE MILITAIRE: 1863 (fl), *Anon. sub Herb. Blackburn s.n.* (K, syntype, 2 sheets). WITHOUT PRECISE LOCALITY: (fl, fr), *Anon. sub Herb. Richard s.n.* (P); (fl), *Anon. sub MAU 1311* (MAU); 1814 (fl, fr), *Carmichael s.n.* (K); ca. 1755 (fl), *Commerson s.n.* (P); (st), *Anon. sub Herb. Ventenat s.n.* (G, 2 sheets).

In terms of floral morphology, *Tambourissa pedicellata* appears to be one of the least specialized species in Mauritius and possibly in the entire genus. It appears to fit best in species Group 5, however. Among Mauritian species, *T. pedicellata* is most similar to *T. amplifolia* which also has long, slender floral pedicels, small subglobose buds and receptacles, and small stamens and styles; the two species have been confused in the past (De Candolle, 1868; Perkins & Gilg, 1901). *Tambourissa amplifolia* is readily distinguishable, however, by its smaller, more slender habit, basal cauliflory, much larger leaves, discoid gynoecious flowers with everted lobes, and androecious flowers deeply split into four flat lobes bearing stamens with apically confluent loculi.

Although *Tambourissa purpurea* (Madagascar) also has monomorphic androecious and gynoecious flowers, it appears to represent a highly specialized condition because of the mucilaginous "hyperstigma" of the gynoecious flowers (see Endress, 1979, 1980b; as *T. religiosa*). The majority of Mauritian species with opposite leaves, more or less open, cupuliform to napiiform or globose gynoecious flowers and conical to setose styles also belonging to Group 5 may have been derived from a common ancestor

which *T. pedicellata* most closely approaches today.

25. ***Tambourissa amplifolia*** (Bojer ex Tul.) A.DC., Prodr. 16(2): 659. 1868; Baker, Fl. Mauritius 287. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901, pro parte; Perk., Pflanzenr. 4, 101 (Nachtr.): 43. 1911. *Mithridatea amplifolia* Bojer, Hortus Maurit. 290. 1837 nom. nud. *Ambora amplifolia* Bojer ex Tul., Monogr. Monim. 299. 1855. TYPE: Mauritius. Woods of Grand Port: Pouce Mountain, Aug. 1851, *Boivin s.n.* (holotype, P).

Monoecious understory treelet or small tree attaining 8 m tall and 9 cm D.B.H., sometimes shrubby, the branches few, erect, the new growth sparsely hirsutulous, the leafy stems terete, 5–14 mm diam., glabrous, the nodes dialated. Leaves often clustered near the ends of the branches, opposite to subopposite, sometimes congested into pseudoverticels of 4, glabrous, petiolate; petioles 14–30 mm by 4–8 mm; lamina chartaceous to subcoriaceous, elliptic to ovate or narrowly ovate, sometimes $\pm$ falcate, 150–450(–500) mm by 80–230(–240) mm, the apex acute to acuminate, the base obtusely decurrent to obtusely cuneate or acutely cuneate to acutely decurrent, the secondary veins 7–9 pairs, making a 60–70° angle with the costa, the venation raised and prominent, visible to 4–5° on both surfaces, the margin plane to slightly revolute; seedling and sucker leaves heterophyllous, with 1–3 pairs of serrate teeth in the apical portion, the petiole red when living. Inflorescence basally cauliflorous (exceptionally ramiflorous), on meristematic swellings up to ca. 1 m above ground level, the flowers solitary, fasciculate or in a unisexual or sexually mixed pleiochasium of 3–7, the gynoecious flower often terminal, the floral axis 5–20(–45) mm by 1.2–2 mm, finely pubescent, basally bracteolate. Androecious flower in bud globose, puberulent, 7–8 mm diam., apiculate with 4 minute tepals, the pedicel 25–60 mm by 0.8–1 mm, pubescent, subtended by a minute, caducous deltoid bracteole; at anthesis deeply 4-fid, 14–18 mm diam., the lobes thick, spreading almost flat or slightly incurved, the internal receptacle surface glabrous; stamens numerous, ca. 100–250, obovoid to clavate, 0.8–1.5 mm long by 0.5–0.6 mm wide, the loculi confluent at the obtuse apex (very rarely separate), occupying the apical $\frac{1}{2}$ – $\frac{2}{3}$ of the stamen, the connective not

prolonged, the filament distinct, slender. Gynoecious flower in bud napiform-discoid, pubescent, the apex depressed, with an apicule or several pairs of minute tepals, the pubescent pedicel 38–80 mm by 1.5 mm; at anthesis shallowly napiform-discoid, 11–13 wide by 4–6 mm long, the apex splitting into 4(–6) everted deltoid lobes, the orifice $\pm$ square or subcircular, comprising ca. $\frac{1}{2}$ total width of the receptacle; styles numerous, ca. 300, shortly conical, 0.6–1 mm long by 0.2–0.3 mm wide basally, the internal receptacle surface velutinous with dense, simple hairs between the styles. Fruiting receptacle solitary at the base of the trunk (exceptionally on the branches), napiform-urceolate or subglobose, 30–56 mm diam. by 22–45 mm long, the orifice ca. 25 mm diam., comprising ca. $\frac{1}{2}$ total width of the receptacle, subentire, bearing remnants of the indurated lobes, the walls ca. 12 mm thick, the external surface corky brown, bumpy, with several prominent veins, the internal surface with numerous shortly conical styles 0.6–1 mm long by 0.2–0.3 mm wide basally, interspersed with scattered simple hairs, the pedicel and peduncle (15–)35–80 mm by 4–5 mm. Mature carpels ovoid-compressed, 12–13 mm long, 6–8 mm wide, 4–5 mm thick, the endocarp light brown, with an irregular network of low ridges, the surface slightly foveate-scrubulate.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. *Tambourissa amplifolia* is local and occasional to common in the lower montane wet forest zone at Bel Ombre (200–400 m), at Plateau Colophane below Macabé Forest (ca. 500 m), on the summit of Mt. Corps de Garde (ca. 750 m), in cloud forest on Mt. Lagrave (500–628 m), and in moist forest on the crest of Piton du Foug (650 m).

MAURITIUS. BEL OMBRE FOREST: Bel Ombre Nature Reserve, 7 Dec. 1971 (fl), *Guého sub MAU 15195* (K, 2 sheets; MAU); 200–400 m, 27 Dec. 1978 (st), *Lorence 2216* (MO); (st), *Lorence 2217* (MO); (st), *Lorence 2218* (MO); (fl), *Lorence 2219* (MO, Z); (fl), *Lorence 2220* (MO, P); (fl), *Lorence 2221* (K, MO); (fl), *Lorence 2222* (K, MAU, MO, REU); (fl), *Lorence 2223* (MO, P); 10 Jan. 1979 (fl), *Lorence 2259* (MAU, MO); 16 Feb. 1979 (fl), *Lorence 2408* (MO); 3 July 1979 (st), *Lorence 2691* (MO, 2 sheets); (fr), *Lorence 2692* (MO). CORPS DE GARDE MT.: summit ridge, $\pm$ stunted forest, 15 Nov. 1973 (fl), *Coode et al. 4066* (K, MAU); 8 Nov. 1971 (fl), *Guého sub MAU 14928* (MAU, 2 sheets). PITON DU FOUGE: crest of Piton du Foug, low, dryish forest, ca. 600 m, 24 Jan. 1976 (fl), *Lorence 1629* (MAU). MACABÉ FOREST: Plateau Colophane below Macabé, ca. 600 m, 15 Jan. 1979 (st), *Lorence 2280*

(MAU, MO); (st), *Lorence 2281* (MO); near Macabé, uplands, ca. 600 m (st), *Vaughan sub MAU 1510* (MAU); Macabé high forest, 660 m, May 1938 (st), *Vaughan sub MAU 1603* (MAU). MT LAGRAVE: 500–600 m, 19 Feb. 1979 (st), *Lorence & Lecordier 2362* (MO). WITHOUT PRECISE LOCALITY: (fl), *Anon. s.n.* (BM); 1863 (fl), *Anon. sub Herb. Blackburn s.n.* (K); (fr), *Anon. sub Herb. Brown s.n.* (K); (fl), *Anon. sub Herb. Cosson s.n.* (P, 2 sheets); 1865 (fl, fr), *Anon. sub Herb. De Candolle 16(2): 659, no. 3* (G, 3 sheets; MO, microfiche); (st), *Anon. sub Herb. Inst. Sci. Madagascar s.n.* (P); (st), *Boivin s.n.* (K, P, possibly isotypes of *T. amplifolia*); 1814 (st), *Carmichael s.n.* (K); ca. 1755 (fr), *Commerson s.n.* (P); (fl), *Commerson 67* (P, 2 sheets); (fl), *s.n. sub Herb. Juss. 16708* (P-JUSS; MO, photo); (st), *Ilardwicke s.n.* (G).

Tambourissa amplifolia belongs to species Group 5 and appears to be most closely related to *T. tau*, which differs in having relatively smaller leaves consistently aggregated into pseudoverticels of two to four pairs separated by long “internodes,” by its T-shaped stamens with separate loculi, and by its long, setose styles, and internally glabrous gynoecious receptacles. Fruiting carpels of *T. amplifolia*, *T. pedicellata*, and *T. tau* all have endocarps with a series of low, $\pm$ branching ridges, a feature unknown in other species and perhaps suggestive of a close affinity between these species.

Bel Ombre forest harbors the largest known population of *Tambourissa amplifolia*, where it occurs sympatrically with *T. tau*. No intermediates or suspected hybrids were found here despite concurrent flowering times from December to February.

Populations that approach *Tambourissa tau*, however, occur in the eastern mountain ranges of Mt. des Créoles (*Lorence & Julien 2337*, MAU, MO) and also Piton Bambou (*Staub sub MAU 13493*, MAU). Although these plants resemble *T. amplifolia* in having large, acuminate petiole leaves, their flowers most closely approach *T. tau* in being axillary (in *Staub sub MAU 13493*) and externally corky brown with multiple, incurved orifice lobes and long, setose styles (in *Lorence & Julien 2337*). Stamens are critical in distinguishing the two species; unfortunately, androecious flowers are absent in both collections. Another intermediate collection, without precise locality (*Anon. sub Herb. Brown s.n.*, K), approaches *T. tau* in having ramiflorous, shortly pedicellate fruits, but the shortly conical styles are characteristic of *T. amplifolia*; androecious flowers are absent also.

The holotype of *Tambourissa amplifolia*, either

from Grand Port or the Pouce Mt., possesses abnormally short floral pedicels (8–10 mm long) and almost glabrous androecious buds. Although lowland forest in the Grand Port region no longer exists, Boivin's type is similar to recent collections from the nearby Mts. Bambous and Des Créoles in some respects. The type's obovate, obtuse stamens with confluent loculi are characteristic of the species as a whole, as are the broad, petiolate leaves, so there can be no doubt as to which species it represents despite the anomalous pedicels and bud pubescence. As *T. amplifolia* and *T. tau* remain morphologically distinct over much of their range, particularly at Bel Ombre where I studied them, I have decided to regard them as distinct species.

Living flowers of *Tambourissa amplifolia* have externally yellow-green to purple-red receptacles, cream to pale orange-yellow stamens, and pale yellow-pink to dark purple styles. A vague, faintly fruity odor is produced by the flowers.

Vernacular name. Bois tambour (Mauritius).

26. ***Tambourissa tau*** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 303, pl. 3, figs. 14, 15. 1982. TYPE: Mauritius. Perrier Nature Reserve: wet forest with *Sideroxylon* dominant, 600 m, 8 Oct. 1978 (fl), Lorence 1835 (holotype, MO; isotypes, B, K, MAU, P, Z).

Little-branched monoecious understory treelet, rarely shrubby, 1–4 m tall, the stems to 75 mm diam., the new growth sparsely puberulent or with rare, scattered hairs, the mature leafy stems glabrous, terete, 4–7 mm diam. Leaves opposite, decussate, clustered into pseudovercels of 2–4 pairs, sessile to subsessile, rarely shortly petiolate, glabrous; petioles stout, 1–8 (–15) mm by 3–6 mm; lamina subcoriaceous to coriaceous, broadly elliptic to narrowly elliptic, obovate or oblanceolate, rarely ovate, (70–)150–300 mm by (30–)45–130 mm, the apex shortly acuminate, shortly acute, obtuse, rounded or retuse, the base subcordate, rounded, obtuse, cuneate or acutely cuneate, the secondary veins (4–)6–9 pairs, making a 50–65° angle with the costa, the venation raised, visible to 3(–4°) adaxially, visible to 4(–5°) abaxially, the margin slightly to moderately revolute; seedling leaves heterophyllous with 2–3 pairs of short, serrate teeth in the apical portion, the petioles red when living. Inflorescence cauliflorous on meristematic swell-

ings along entire length of the stem, occasionally ramiflorous or axillary, the flowers solitary, in a fascicle or dichasium of 2–3, or rarely in a short pleiochasium of 3–6 flowers, sexually mixed or not, the floral axis 2–3(–5) mm by 1–1.5 mm, $\pm$ corky, glabrous or sparsely puberulent basally, subtended by several small, ciliate, naviculate-deltoid bracteoles. Androecious flower in bud globose, $\pm$ depressed, the apex with several minute, deltoid tepals, the external surface corky brown, mottled, the pedicel 6–20 mm by 1–1.5 mm, basally bracteolate; at anthesis 4–6-fid, 20–25 mm diam., the lobes spreading flat, the internal receptacle surface glabrous; stamens numerous, ca. 100–150, T-shaped, 1–1.5 mm long by 1.5–2 mm wide, the loculi separate on lateral arms (rarely $\pm$ sessile, but never confluent), the filament distinct, slender, the connective slightly prolonged apically or not. Gynoecious flower in bud turbinate-depressed to napiform-depressed, 7–10 mm diam. by 4–5 mm long, externally corky brown, apiculate with several minute tepals, the pedicel 6–20(–40) mm by 1–1.5 mm, subtended by several pairs of deltoid bracteoles; at anthesis napiform-urceolate, 10–12 mm diam., the orifice splitting into 5–10 thick, irregularly deltoid, straight or incurved lobes, the orifice 3–6 mm diam., comprising ca. $\frac{1}{3}$ – $\frac{1}{2}$ total width of receptacle; styles numerous, ca. 80–100, slender, setose, 2–3 mm long by 0.3–0.5 mm wide at the ventricose base, the internal receptacle surface glabrous. Fruiting receptacle solitary on the main stem or major branches, rarely axillary or subterminal, shallowly cupuliform-patelliform to subglobose, 25–50 mm diam. by 10–27 mm long, the orifice 10–26 mm diam., comprising ca. $\frac{1}{2}$ total width of the receptacle, subentire with 5–6 indurated deltoid lobes, the walls 10–14 mm thick, the external surface corky brown, bumpy, the internal surface with numerous scattered, setose styles 1.5–3.5 mm long by 0.3–0.4 wide basally, otherwise glabrous, the pedicel stout, 8–20 mm by 2–7 mm. Mature carpels ovoid-compressed, 10–14 mm long, 6–8 mm wide, 4–6 mm thick, with occasional low, irregular ridges, the surface scrobiculate to foveate. Gametic chromosome number, $n = 19$. Figure 39.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. This is one of the commonest and most widespread members of the genus in Mauritius, occurring in most medium to upper altitude wet and cloud forest communities from ca. 300 to 800 m.

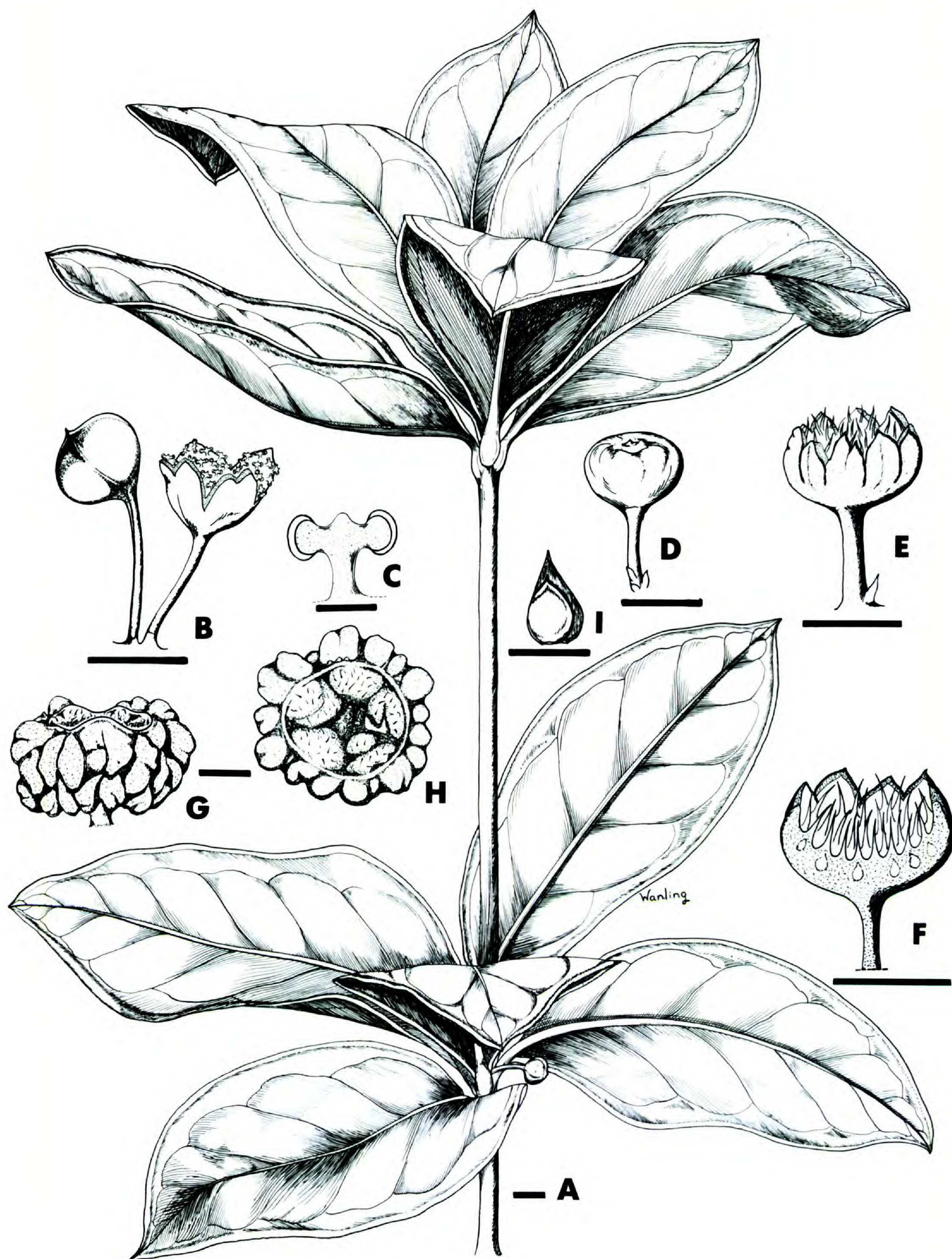


FIGURE 39. *Tambourissa tau* Lorence.—A. Habit.—B. Androecious bud and newly opened androecious flower, lateral view.—C. Stamen, lateral view.—D. Gynoecious flower in bud, lateral view.—E. Gynoecious flower at anthesis, lateral view.—F. Gynoecious flower, longitudinal section.—G. Submature fruiting receptacle, lateral view.—H. As in G, apical view.—I. Fruiting carpel, lateral view. A. Perrier Nature Reserve, Mauritius (Lorence photo, unvouchered). B–F. Lorence 1835 (MO). G, H. Lorence 2950 (MO). I. Lorence 2629 (MO). Bars equal 10 mm in A, B, D–I, and 1 mm in C.

MAURITIUS. BASSIN BLANC: side of track to E side of lake, 550 m, 25 May 1976 (fr), *Richardson et al.* 4163 (K). BEL OMBRE FOREST: ca. 200–400 m, 27 Dec. 1978 (fl), *Lorence* 2215 (MO); 10 Jan. 1979 (fl), *Lorence* 2257 (MO); (fl), *Lorence* 2258 (MO). CUREPIPE BOTANICAL GARDEN: near lake, 30 June 1966 (fl), *Vaughan sub MAU 12203* (MAU, 3 sheets). GAULETTES SERRÉES: low mixed wet forest over lava, 400–450 m, 19 May 1979 (fl), *Lorence et al.* 2641 (MO). GRAND BASSIN: upland thicket, 22 Sept. 1932 (st), *Orian sub MAU 47* (MAU). MACABÉ FOREST: high forest, 660 m, 18 Oct. 1978 (fl), *Lorence et al.* 1863 (MO); Macabé to Brise Fer road, 660 m, 8 Dec. 1978 (fl), *Lorence* 2102 (MAU, MO); (fr), *Lorence* 2103 (MO); Mare Longue to Macabé road, low indigenous thicket, 1 Nov. 1962 (fl), *Vaughan sub MAU 10472* (MAU). MIDLANDS: vestige of indigenous vegetation along river, 400 m, 9 Feb. 1979 (fl), *Lorence & Lecordier* 2357 (MO). MONTAGNE COCOTTE: cloud forest, 770 m, 1 Dec. 1978 (st), *Lorence* 1975 (MO); (fl), *Lorence* 1976 (MAU, MO); (fl), *Lorence* 1977 (MAU, MO); 19 Dec. 1978 (fl), *Lorence & Lecordier* 2161 (MAU, MO); (st), *Lorence & Lecordier* 2165 (MO). MONTAGNE DES CRÉOLES: transitional evergreen forest, 250–300 m, 25 Jan. 1979 (fl), *Lorence & Julien* 2337 (MAU, MO); (st), *Lorence & Julien s.n.* (MAU). MONTAGNE LAGRAVE: flank facing Eau Bleue reservoir, 5 Apr. 1974 (fr), *Coode et al. sub MAU 17615* (MAU); N part, summit area, degraded cloud forest invaded by exotics, 500–600 m, 9 Feb. 1979 (fl), *Lorence & Lecordier* 2363 (MO); S slope facing Eau Bleue reservoir, cloud forest invaded by exotics, 600 m, 24 May 1979 (fr), *Lorence & Lecordier* 2649 (MO). PERRIER NATURE RESERVE: dense indigenous thicket, 14 May 1970 (fr), *Guého sub MAU 14297* (MAU); lower montane wet forest, ca. 600 m, 8 Oct. 1978 (fl), *Lorence* 1836 (MO); (fl), *Lorence* 1837 (MO); 13 Oct. 1978 (st), *Lorence* 1841 (MO); 12 May 1979 (fr), *Lorence* 2628 (K, MAU, MO, P); (fr), *Lorence* 2629 (MO); Perrier near Mare aux Vacoas, 10 Sept. 1937 (st), *Vaughan sub MAU 1404* (MAU); 25 Oct. 1962 (fl), *Vaughan sub MAU 10473* (MAU). PÉTRIN NATURE RESERVE: low *Sideroxylon* wet forest, 630 m, 12 Dec. 1978 (fl), *Lorence* 2122 (MAU, MO). PITON BAMBOU: near crest of hill on the leeward side, 14 Aug. 1968 (fl), *Staub sub MAU 13493* (MAU; approaches *T. amplifolia*). PITON DE LA RIVIÈRE NOIRE: lower montane wet forest, 700–827 m, 25 Nov. 1978 (fl), *Lorence* 1964 (MAU, MO); 26 Dec. 1978 (fl), *Lorence* 2204 (MO). PLAINE LIEVRE: by side of road to Brise Fer, indigenous thicket, 9 Mar. 1969 (fr), *Guého sub MAU 13750* (MAU); stunted forest around clearing, 600 m, 27 Aug. 1979 (fl), *Lorence et al.* 2923 (K, MO). VALLEY OF CASCADE 500 PIEDS: *Calophyllum*/Sapotaceae wet forest, 550 m, 18 May 1979 (fl), *Lorence* 2634 (MO). WITHOUT PRECISE LOCALITY: (fr), *Anon. sub Herb. Richard s.n.* (P); 14 Jan. 1930 (fl, fr), *Vaughan* 382 (K, 3 sheets).

Tambourissa tau is most closely allied to *T. amplifolia*, with which it has been confused in the past (e.g., Vaughan & Wiehe, 1937, 1941, in their vegetational sampling analyses at Mt. Cocotte, Macabé Forest and Perrier). Both belong to species Group 5 and have large leaves, making them difficult to separate vegetatively, although

they are easily separable by floral characters. *Tambourissa amplifolia* has pubescent inflorescences, internally velutinous gynoeceous flowers with shorter, non setose styles, and apically confluent anther loculi never found in *T. tau* (see *T. amplifolia* for further discussion). The specific epithet *tau* is Greek, Latin, and Celtic for “T,” referring to the characteristically T-shaped stamens which are unique in the entire genus.

A plant growing in the Curepipe Botanical Garden (*Vaughan sub MAU 12203*, MAU) is typical of *Tambourissa tau* in all characters except the anomalous staminal loculi, which are sessile and not borne on extended lateral arms, although neither are they apically confluent as in *T. amplifolia*. Furthermore, gynoeceous flowers of *Vaughan sub MAU 12203* are typical of *T. tau*. Flynn and Rowley (1972) studied the ultrastructural development of the pollen wall of this same plant as *T. amplifolia*.

Flower color morphs with either dark reddish purple or pale pink to greenish white stamens and styles occur; these are generally constant within a given population (e.g., dark red-purple as Perrier, pale pink or white at Mt. Cocotte). The flowers produce no apparent odor.

Vernacular name. Bois tambour (Mauritius).

27. ***Tambourissa tetragona*** (Boiv. ex Tul.) A.DC., Prodr. 16(2): 659. 1868; Baker, Fl. Mauritius 289. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 70. 1901. *Ambora tetragona* Boiv. ex Tul., Ann. Sci. Nat. (Paris) 4(3): 30. 1855; Tul., Monogr. Monim. 302. 1855. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1755) (st), *Commerson s.n.* (lectotype, P, here designated).

Dioecious (?), sparsely branching slender treelet or small tree attaining 6 m tall and 10 cm D.B.H., the bark pale brown, smooth with longitudinal fissures, the new growth glabrous, the mature leafy stems quadrangular, 4–6 mm diam., with 4 low wings ca. 1–1.5 mm wide. Leaves opposite, rarely subopposite, petiolate, glabrous; petioles stout, 5–15 mm by 2–3 mm, winged, the wings decurrent onto the stem; lamina subcoriaceous, narrowly obovate, oblanceolate, narrowly oblong or rarely narrowly elliptic, 52–180 mm by 17–48 mm, the apex shortly acuminate, rarely shortly acute, the tip indurated, the base acute, strongly decurrent along the petiole, the

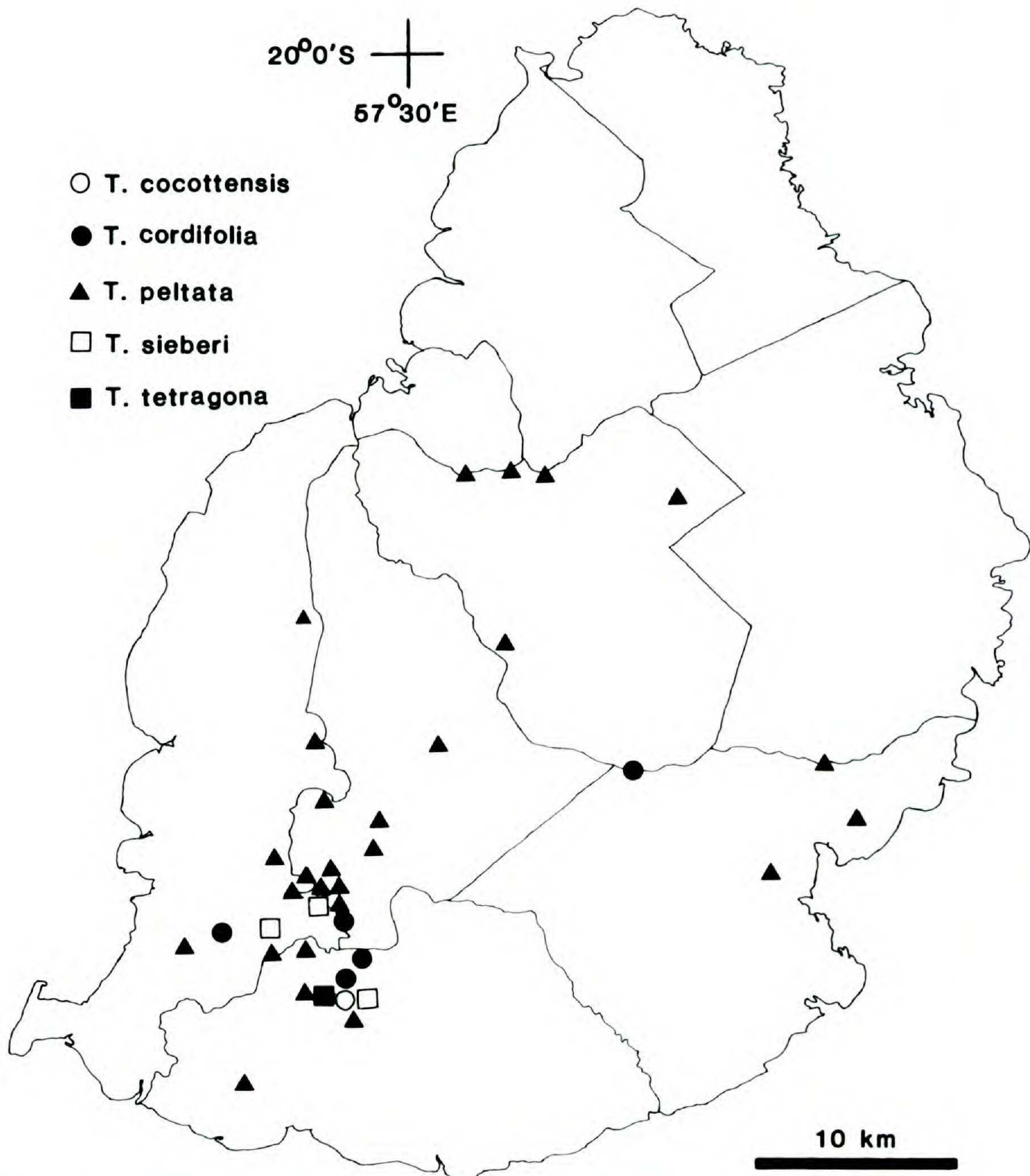


FIGURE 40. Distribution map of some *Tambourissa* species in Mauritius.

secondary veins 8–13 pairs, making a 65–80° angle with the costa, the venation obscure, visible to 2° on both surfaces, the margin revolute. Cauliflorous, the androecious inflorescence (fide Tulasne) a sparse pleiochasium, the buds globose, inaperturate, shortly pedicellate, the stamens and mature androecious flowers unknown; gynoecious inflorescence a short, glabrous, rarely leafy pleiochasium of 5–11 flowers, the floral axis quadrangular, 7–13 mm by 2–2.5 mm, subtended by several pairs of glabrous, decussate naviculate bracteoles 1 mm by 0.5 mm, the pedicel 3–4 mm by 1.5–2 mm, subtended by a glabrous, deltoid bracteole 1–2.5 mm long. Gynoecious flower in bud napiform-depressed, 8–10 mm diam. by 6–8 mm long, apiculate with 4 small,

glabrous obtuse tepals, the external surface drying wrinkled, glabrous, the walls thick; at anthesis the apex splitting into 4(–5) deltoid lobes ca. 3 mm long and wide, the orifice small, ca. 1 mm wide, X-shaped, the lobes hirsute internally; styles numerous, ca. 200, shortly conical, 0.6–0.8 mm long by 0.5–0.7 mm wide at the strongly ventricose base, the internal receptacle surface glabrous between the styles. Fruiting receptacle and carpels unknown.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa tetragona* is presently known only from low cloud forest on the summit of Mt. Cocotte at the southern extremity of the central plateau.

MAURITIUS. GRAND PORT: woods of the Grand Port District, Aug. 1851 (st), *Boivin s.n.* (P, syntype). MONTAGNE COCOTTE: Aug. 1977 (st), *Friedmann 3201* (P); summit, 11 Dec. 1979 (st), *Guého & Lecordier sub MAU 19501* (MAU); low, degraded cloud forest on summit, 770 m, 19 Dec. 1978 (st), *Lorence & Lecordier 2164* (MO); (st), *Lorence & Lecordier 2166* (K, MAU, MO); 17 Jan. 1979 (st), *Lorence 2286* (MO); 30 Aug. 1979 (fl), *Lorence et al. 2928* (MO); Dec. 1937 (fl), *Vaughan sub MAU 1508* (MAU); (fl), *Vaughan sub MAU 1706* (MAU). WITHOUT PRECISE LOCALITY: (st), *Anon. sub Herb. Richard s.n.* (P).

The leaves, female receptacle, and styles of *Tambourissa tetragona* are morphologically similar to those of *T. cocottensis*, a species also confined to a small patch of cloud forest on the summit of Mt. Cocotte, one of the island's highest and wettest spots. Although androecious flowers and fruiting receptacles of the former are required to further assess its affinity, both belong to species Group 5. The distinctive quadrangular, winged stems of *T. tetragona*, however, set it apart from all other members of the genus.

In the living state, leaves of *Tambourissa tetragona* have a lustrous, dark green lamina and red petiole, the stems being pale green with translucent wings. Vegetatively, it is one of the most attractive members of the genus. Gynoecious buds are shiny green flushed with dark red-purple. Buds are initiated in July and August and appear to mature in December. Known only from a single, small population in a highly degraded habitat, the species should be considered endangered. My attempts to propagate it vegetatively by cuttings failed.

Vernacular name. Bois tambour (Mauritius).

28. ***Tambourissa cocottensis*** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 295, pl. 1, fig. 2. 1982. TYPE: Mauritius. Low cloud forest, summit of Mt. Cocotte, 760 m, 19 Dec. 1978 (fl, fr), *Lorence & Lecordier 2167* (holotype, MO; isotype, MAU).

Monoecious treelet or small tree 4–5 m tall and 10–35 cm D.B.H., often multistemmed from coppices, the new growth glabrous, the mature leafy stems terete, 2–4 mm diam., longitudinally striate. Leaves opposite to subopposite, petiolate, glabrous; petioles 7–20 mm by 1–2 mm; lamina subcoriaceous, elliptic, 45–105 mm by 15–40 mm, the apex shortly acute to shortly acuminate, the tip indurated, the base acutely cuneate, slightly decurrent, the secondary veins 6–9 pairs, mak-

ing a 55–65° angle with the costa, the venation visible to 3° on both surfaces, slightly raised, the margin moderately revolute. Androecious flowers solitary or in fascicles of 2, borne along the trunk. Androecious flower in bud globose, apiculate, 6 mm diam., externally corky brown, the pedicel and peduncle 4–5 mm by 1.5 mm, quadrangular, pilose, bearing 4 decussate rows of bracteoles 1 mm long; at anthesis 4–7-fid, the lobes spreading flat, 20–21 mm diam., reddish pink; stamens ca. 150–200, subsessile, linear-subulate, 3 mm by 0.6–0.8 mm, the loculi lateral, free, occupying ca. $\frac{2}{3}$ – $\frac{3}{4}$ total length of stamen, the connective prolonged, slender, 1 mm long, the internal receptacle surface glabrous. Gynoecious inflorescence cauliflorous from meristematic swellings along the basal 1 m of the trunk, the flowers solitary or in fascicles of 2. Gynoecious flower in bud napiform-depressed, 9–11 mm diam. by 5–7 mm long, the apex bearing 3–4 minute, pubescent deltoid tepals, the external receptacle surface pale corky brown with scattered simple hairs, the pedicel and peduncle 4–7 mm by 1–1.5 mm, jointed near the base, quadrangular, pilose, bearing 4 decussate rows of minute, ciliate naviculate bracteoles 1–1.5 mm long; at anthesis the apex splitting into 5–7 irregular, $\pm$ inflexed deltoid lobes, the orifice comprising ca. $\frac{1}{3}$ total width of the receptacle; styles numerous, ca. 150–200, narrowly conical, setose, 1.5–2 mm long by 0.2–0.3 mm diam. at the slightly ventricose base, the apex long acuminate, the internal receptacle surface with scattered clusters of simple hairs between the styles. Young, submature fruiting receptacle globose-urceolate, 15 mm diam. by 12 mm long, the apex depressed, the orifice subcircular, 3–4 mm diam., with 5–7 thick, deltoid lobes, comprising ca. $\frac{1}{4}$ – $\frac{1}{5}$ total width of the receptacle, the external surface mottled corky brown, the internal surface with numerous setose styles 1.5–2 mm long by 0.5 mm wide basally, pilose between the styles and on the lobes, the peduncle and pedicel 5 mm by 3 mm. Mature fruiting receptacle and carpels unknown. Figure 41.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa cocottensis* is known only from a single population on the summit of Mt. Cocotte in low cloud forest (annual precipitation 5,000 mm). Extensive searching revealed only four individuals growing within an area ca. 100 m across.

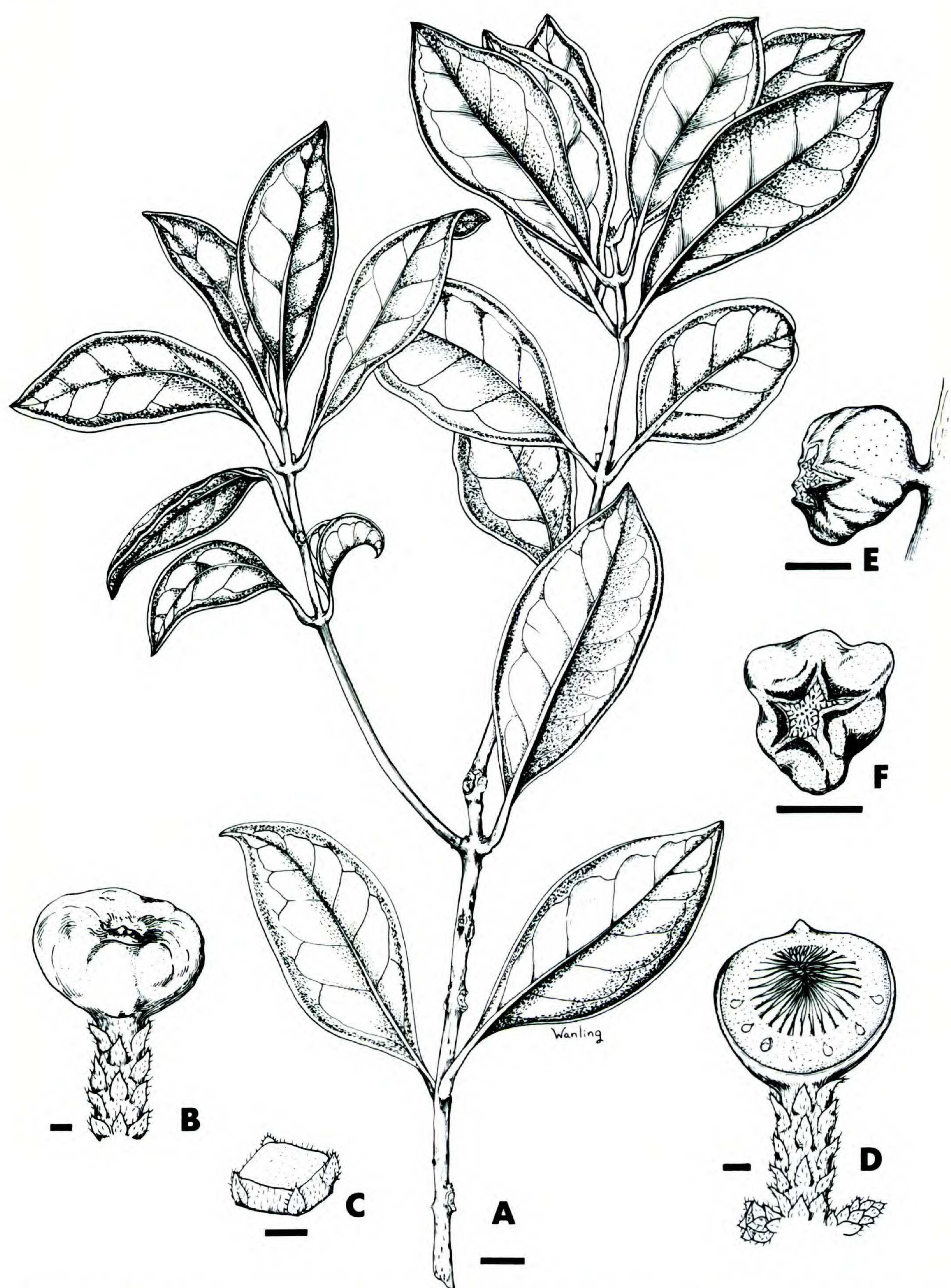


FIGURE 41. *Tambourissa cocottensis* Lorence.—A. Habit.—B. Gynoecious flower in bud, lateral view.—C. Gynoecious floral pedicel, transverse section.—D. Gynoecious flower in bud, longitudinal section.—E. Submature fruiting receptacle, lateral view.—F. As for E, apical view. A. Lorence 2288 (MO). B–D. Lorence 2287 (MO). E, F. Lorence 2167 (MO). Bars equal 10 mm in A, E, F, and 1 mm in B–D.

MAURITIUS. MONTAGNE COCOTTE: summit region, low degraded cloud forest, 760 m, 17 Jan. 1979 (fr), *Lorence* 2287 (K, MO, P); (st), *Lorence* 2288 (MO); crest, 14 July 1982 (fl), *Lecordier* sub MAU 20412 (MAU); 23 Sept. 1983 (fl), *Lecordier & Strahm* sub MAU 20563 (MAU).

Tambourissa cocottensis closely resembles *T. tetragona* in a number of respects, including leaf size, shape, texture, margin, and venation, but lacks the winged stems and petioles of the latter. Both are cauliflorous with structurally similar flowers, but those of *T. cocottensis* are solitary or in fascicles of two and externally corky, differing from the smooth, glabrous pleiochasial flowers of *T. tetragona*. They more closely resemble those of *T. tau*, except for the distinctive quadrangular floral pedicels bearing four decussate rows of ciliate bracteoles. Both *T. cocottensis* and *T. tetragona* belong to species Group 5, although the prolonged staminal connectives of the latter are suggestive of certain Madagascan species.

The four known individuals of *Tambourissa cocottensis* are of different size classes, suggesting some regeneration has taken place in recent years. The two largest individuals (both gynoeceous) were in bud in August 1979, and young fruits were present in December 1978 and January 1979; androeceous flowers were not found. Although officially a nature reserve, the forest on Mt. Cocotte is highly degraded and has undergone extensive invasion by vigorous, weedy exotic plant species. As a result, there is a grave danger that the population is too small to maintain itself, as is also the case for *T. tetragona*. Both appear to be relictual species confined to the summit of Mt. Cocotte.

- 29. *Tambourissa cordifolia*** Lorence, Bull. Mus. Hist. Nat. (Paris), Ser. 4, Sect. B, Adansonia 3(3): 296, pl. 1, figs. 5, 6. 1982. TYPE: Mauritius. Pétrin Nature Reserve: low *Philippia* heath formation, 630 m, 15 May 1979 (fl, fr), *Lorence* 2631 (holotype, MO; isotype, K).

Glabrous dioecious shrub, rarely a small treelet, the multiple erect stems 50–200 cm tall and 6–10 mm diam., the mature leafy stems 2–4 mm diam., longitudinally striate. Leaves opposite, decussate, subsessile or sessile, glabrous; petiole 1–1.5 mm long by 2–3 mm wide; lamina subcoriaceous, ovate to elliptic, 30–80 by 25–55 mm, the apex shortly acute, obtuse or retuse, often

rounded or mucronulate, the base cordate, rarely subtruncate, the secondary veins 5–6 pairs, making a 50–60° angle with the costa, the venation raised and visible to 3(–4°) adaxially and to 4(–5°) abaxially, the margin slightly revolute; seedling leaves heterophyllous, the petioles short, red when living, the lamina narrowly elliptic, entire or with 1–2 pairs of small teeth apically. Inflorescence glabrous, either ramiflorous on leafless nodes or cauliflorous, the flowers solitary or in fascicles of 2(–3), very rarely in a short di- or pleiochasium of 3(–5) flowers, or the flowers rarely solitary and axillary or terminal on leafy shoots. Androeceous flower in bud globose, 10–16 mm diam., the apex with 4 minute, obtusely deltoid tepals, the pedicel and peduncle jointed basally, 9–30(–50) mm by 1–1.5 mm, bearing basally 1–3 pairs of apically ciliate, deltoid bracteoles; at anthesis 4(–5)-fid, 28–36 mm diam., the lobes spreading flat, then reflexing; stamens numerous, ca. 300–400, narrowly ellipsoid or clavate, 1–2 mm by 0.5–1 mm, the loculi occupying $\frac{1}{2}$ – $\frac{3}{4}$ total length of the stamen, usually separate, sometimes confluent basally into a U-shape, or confluent apically at the obcordate apex, the connective not prolonged, the internal receptacle surface bearing scattered hairs. Gynoeceous flower in bud nappiform-depressed, apiculate with 4 minute tepals, the pedicel and peduncle jointed basally, 10–15 mm by 1–1.5 mm, basally bracteolate as in male flower; at anthesis shallowly nappiform-urceolate, 8–12 mm diam. by 4–6 mm long, the orifice splitting into 4(–6) outcurved deltoid lobes, 5–8 mm diam., comprising $\frac{1}{2}$ – $\frac{2}{3}$ total width of the receptacle, the internal surface of the lobes shallowly rugose, glabrous; styles numerous, ca. 100–400, shortly conical, 0.8–1 mm long by 0.4–0.5 mm wide basally, the apex papillose, the internal receptacle surface with clusters of simple hairs between the styles. Fruiting receptacle solitary on the stems, patelliform to shallowly cupuliform, 25–60 mm diam. by 13–40 mm long, the orifice 16–40 mm diam., comprising $\frac{1}{2}$ – $\frac{3}{4}$ total width of the receptacle, the rim subentire with 4–6 indurated deltoid lobes, the walls 8–12 mm thick, the external surface corky brown, the internal surface with numerous short, conical styles 0.5–1 mm long by 0.5 mm wide basally, interspersed with clusters of hairs, the pedicel and peduncle 16–25 mm by 2–3 mm. Mature carpels 12–13 mm long, 6–8 mm wide, 5–6 mm thick, ovoid-compressed, the endocarp dark brown, the surface scrobiculate. Gametic chromosome number, $n = 19$. Figure 42.

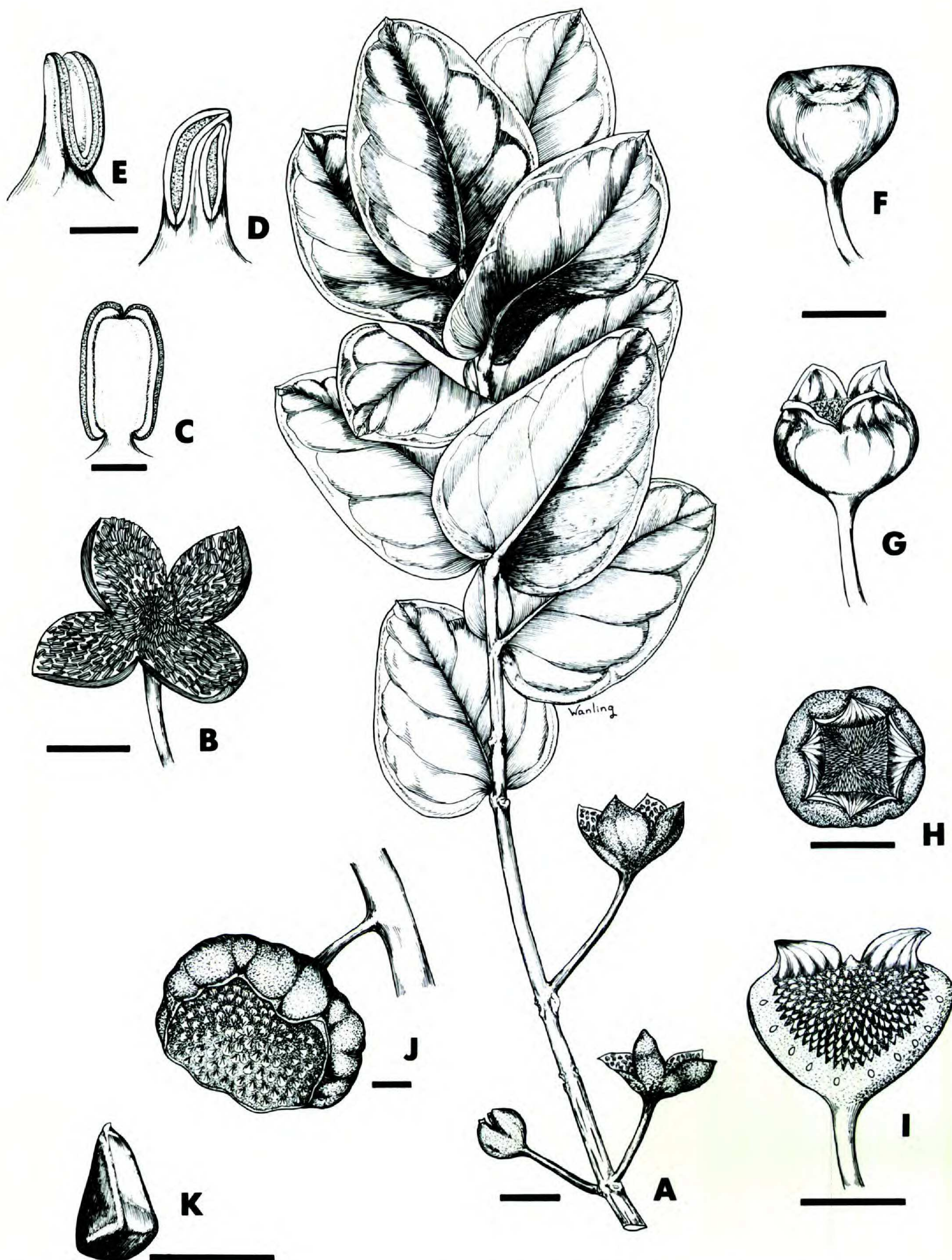


FIGURE 42. *Tambourissa cordifolia* Lorence.—A. Habit, male.—B. Androecious flower at anthesis, apical view.—C. Stamen with free loculi, abaxial view.—D. Stamen with free loculi, adaxial view.—E. Stamen with basally confluent loculi, adaxial view.—F. Gynoecious flower in bud, lateral view.—G. Gynoecious flower at anthesis, lateral view.—H. Gynoecious flower at anthesis, apical view.—I. Gynoecious flower at anthesis, longitudinal section.—J. Submature fructing receptacle.—K. Fructing carpel, lateral view. A–E. Lorence 2632 (MO). F–I. Lorence 2630 (MO). J, K. Lorence 2631 (MO). Bars equal 10 mm in A, B, F–K, and 1 mm in C–E.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. *Tambourissa cordifolia* is restricted to upland regions of hard, unweathered ground water laterite or "cui rasse" supporting low scrub formations, often of *Philippia* heath. It is particularly abundant at Pétrin (630 m, annual precipitation 4,000 mm), and also occurs in comparable *Philippia* heath on Mt. Laselle (550 m, annual precipitation 4,500 mm), in low, marshy scrub at Les Mares near the base of Mt. Cocotte (650 m, annual precipitation 4,800 mm), at Crown Land Declerc, and in low thicket near the summit of Piton de la Rivière Noire (827 m, annual precipitation 4,200 mm).

MAURITIUS. CROWN LAND DECLERC: 15 Aug. 1968 (fl), *Vaughan sub MAU 13343* (MAU). LES MARES: track from Plaine Paule to Mt. Cocotte, 650 m, 13 May 1979 (fl), *Lorence 2626* (MO); 10 Aug. 1979 (fl), *Lorence 2894* (MO). MARE LONGUE PLATEAU: June 1977 (fl), *Friedmann 3132* (P). MONTAGNE LASELLE: N flank, 4 Oct. 1973 (fl), *Lorence sub MAU 16282* (MAU); Midlands, exposed situations, Mar. 1931 (fr), *Vaughan sub MAU 729* (MAU). PÉTRIN NATURE RESERVE: low indigenous thicket, 2 June 1971 (fr), *Guého sub MAU 14762* (MAU); *Phyllica/Philippia* heath on lateritic soil, Oct. 1975 (fl), *Guého sub MAU 17585* (MAU, 2 sheets); indigenous thicket near Pétrin, 2,150 ft. (630 m), 23 Mar. 1963 (fr), *Lalouette sub MAU 10337* (MAU); low *Philippia* heath formation, 630 m, 23 Apr. 1973 (fl), *Lorence M 113* (K, MO); (fl, fr), *Lorence M 114* (K, 2 sheets; MO); 26 May 1973 (fl), *Lorence M 144* (K, MO); 12 Dec. 1978 (fr), *Lorence 2119* (MAU, MO); 10 Feb. 1979 (fr), *Lorence 2378* (MAU, MO, P); 4 Apr. 1979 (fl), *Lorence 2571* (MO); 15 Apr. 1979 (fr), *Lorence 2595* (MAU, MO); 9 May 1979 (fl), *Lorence 2618* (MO); 12 May 1979 (fl), *Lorence 2623* (MO); 15 May 1979 (fr), *Lorence 2630* (MO); (fl), *Lorence 2632* (MAU, MO); 22 May 1979 (fl), *Lorence 2645* (MO, P, Z); (fr), *Lorence 2646* (MO); 19 June 1979 (st), *Lorence 2660* (MO); 1 May 1976 (fl), *Richardson et al. 4074* (K); (fl), *Richardson et al. 4075* (K); (fr), *Richardson et al. 4076* (K); (fr), *Richardson et al. 4077* (K); Crown Land Pétrin, 17 June 1939 (fl), *Vaughan sub MAU s.n.* (MAU); (fr), *Vaughan 729* (MAU); Aug. 1937 (fl), *Vaughan sub MAU 1400* (MAU, 2 sheets); 6 June 1969 (fl, fr), *Vaughan sub MAU 13776* (MAU). PITON DE LA RIVIÈRE NOIRE: (fl), *Randabel sub MAU 679* (MAU). WITHOUT PRECISE LOCALITY: (st), right hand leafy collection only, *Anon. sub MAU 1314* (MAU).

Its sessile, cordate leaves and shrubby habit are presumably adaptations to the unique ecological niche which *Tambourissa cordifolia* occupies. Among other Mascarene species of the genus, it appears to be most closely allied to *T. amplifolia* in terms of floral morphology. Both are cauliflorous (rarely ramiflorous) species with long pedicellate, often solitary flowers, the androecious flowers being 4-fid, internally white, and having numerous clavate stamens, the gy-

noecious receptacles being napiform, opening by 4(-6) everted deltoid lobes, and having numerous short, conical styles interspersed with hairs. *Tambourissa amplifolia* is readily distinguishable by its larger habit, basal cauliflory, monoecy, pubescent inflorescences with longer pedicels and smaller floral receptacles, and very much larger, non-cordate petiolate leaves. Both belong to species Group 5.

The only other dioecious Mauritian species besides *Tambourissa cordifolia* is *T. peltata*, which has ternate to subalternate leaves and belongs to species Group 9. Although the two species are known to hybridize naturally, at least one such hybrid (*Lorence 2624*, MO) is highly sterile with ca. 95% aborted pollen grains.

In living material, the flower buds and outer surface of the receptacle are cream or yellowish flushed with purple-red. The inner, staminal surface of the androecious flowers and lobes of the gynoecious flowers are creamy white and the styles purple-red. Flowers of both sexes produce strong, fruity odors akin to that of ripe apricots or stewed ripe bananas.

Vernacular name. Bois tambour (Mauritius).

30. *Tambourissa sieberi* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Baker, Fl. Mauritius 287. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 68. 1901; Vaughan, Mauritius Inst. Bull. 1(1): 76. 1937. *Ambora sieberi* Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 304. 1855. TYPE: Mauritius. Without precise locality (ca. 1822) (fl), *Sieber Fl. Maurit. II, 316* (holotype, P; isotypes, G, K).

A. vestita Tul., Ann. Sci. Nat. (Paris) 4(3): 31. 1855; Tul., Monogr. Monim. 306. 1855. *Tambourissa vestita* (Tul.) A.DC., Prodr. 16(2): 660. 1868; Cordem., Fl. Réunion 301. 1895; Perk. & Gilg, Pflanzenr. 4, 101: 69. 1901. TYPE: "Bourbon?" (probably Mauritius), without precise locality (ca. 1755), *Commerson s.n.* (holotype, P).

Monoecious tree 10-15 m tall and 30-40 cm D.B.H., the bark light brown, flaking, the new growth velutinous-tomentose with simple, yellowish wavy hairs, the mature leafy stems velutinous, terete, 2-5 mm diam. Leaves opposite to subopposite, petiolate; petioles velutinous, 5-15 mm by 1-1.5 mm; lamina chartaceous to subcoriaceous, both surfaces tomentose-pubescent when young, adaxially glabrescent, elliptic to

broadly elliptic, rarely obovate or suborbiculate, 40–76 mm by 18–40 mm, the apex shortly acuminate, acute, rarely obtuse, the base acutely cuneate to acute, the secondary veins 4–7 pairs, making a 60–70° angle with the costa, the venation visible to 2(–3°) adaxially, and to 3(–4°) abaxially, the margin revolute. Inflorescence cauliflorous on mid to upper part of the trunk and on the major branches, an erect, generally unisexual, rarely leafy thyrse of 16–90 flowers, irregularly branching to 2(–3°), all parts pale yellowish velutinous-tomentose, the floral axis stout, 50–310 mm by 3–8 mm, flattened and dilated at the nodes, the secondary axes opposite to subopposite, $\pm$ ascendant, 6–90 mm by 2–4 mm, the ultimate branches bearing cymose units of 1–4 flowers, the buds of both sexes globose, 12–14 mm diam., velutinous, apiculate, the apex crowned with 2–3 pairs of persistent, decussate velutinous naviculate tepals 1.5–2.5 mm long by 1 mm wide, the pedicels and peduncles often subtended by a subulate, velutinous caducous bracteole 2–3 mm long, or rarely by a leaf, the pedicels 10–25 mm by 1.5–2 mm. Androecious flower at anthesis deeply (4–)5(–6)-fid, 25–35 mm diam., the lobes spreading flat; stamens numerous, ca. 100–140, ovoid to ellipsoid or oblong, 2–5 mm long by 1–2 mm wide, subsessile, the loculi lateral, separate, occupying almost the entire length of the stamen, the filament broad, short or sessile, the connective broad, slightly prolonged or not, the apex obtuse to emarginate, the internal receptacle surface glabrous. Gynoecious flower at anthesis globose, 15–18 mm diam., the orifice subcircular, 2–4 mm diam., with 4–6 irregular, shallow lobes; styles numerous, ca. 850–875, narrowly conical to setose, 3–4 mm long by 0.4–0.5 mm wide basally, coalescent into groups of 12–30, the internal receptacle surface densely velutinous between the styles. Fruiting receptacles produced on the trunk and major branches, in clusters of 3–15, the major axis 15–20 mm diam., woody, the secondary axis ca. 12 mm diam., the pedicel and peduncle 10–35 mm long by 6–15 mm diam., the receptacle irregularly globose-urceolate, depressed, 55–160 mm diam. by 35–75 mm long, the orifice small, comprising ca. $\frac{1}{4}$ – $\frac{1}{3}$ total width of the receptacle, the walls 18–20 mm thick, externally pale corky brown, internally with numerous setose styles 2.5–3.5 mm long by 0.5–0.6 mm wide basally, the sides channelled, the surface sparsely tomentose between the styles. Mature carpels ovoid-compressed, 10–13 mm long, 6–7 mm wide, 4–

5 mm thick, the smooth endocarp pale brown. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. Isolated individuals and small populations of *Tambourissa sieberi* are known from mature wet forest at Macabé (660 m) and in the Black River Gorges (400–500 m) where the annual precipitation is ca. 3,200–3,400 mm, and also from low cloud forest on Mt. Cocotte (650–760 m, annual precipitation ca. 5,000 mm). Although the species appears to set fruit readily and several seedlings presumably of *T. sieberi* were found at Mt. Cocotte, no recent regeneration was observed at any of the other sites, undoubtedly due to severe competition pressures exerted by vigorously invasive exotic species.

Although Tulasne thought that the sterile type of *Ambora vestita* may have been collected in Réunion (formerly Bourbon) by Commerson, he in fact questioned the origin of the specimen. Commerson actually did collect in Réunion (Ly-Tio-Fane, 1976), but a number of his other collections are wrongly labelled. I therefore suspect that the type of *Tambourissa vestita* is actually from Mauritius where he collected more extensively. That the type of *T. sieberi* lacks leaves also seems to have prompted Tulasne to describe the Commerson specimen as a new species. In any case, no tomentose *Tambourissa* has ever been subsequently collected or noted from Réunion (Cordemoy, 1895; Rivals, in herb.; Cadet, pers. comm.). Because the type of *T. vestita* is indistinguishable from material of *T. sieberi*, I consider the species synonymous and have chosen to retain the latter name because the type has flowers and is more widely distributed in herbaria.

MAURITIUS. BLACK RIVER GORGES: 1 Dec. 1933 (fl), *Carcenac sub MAU 794* (MAU); Crown Land Le Bouton in Black River Gorges, primary wet forest, ca. 400 m, 10 Jan. 1976 (fl), *Lorence 1585* (K, 2 sheets; MAU, 2 sheets; MO). MACABÉ FOREST: (fl) (prob. Dec. 1973), *Bernardi sub MAU 12873* (G, MAU); Plateau Macabé, 12 Mar. 1933 (fl), *Carcenac 48 sub MAU 1313* (MAU); Crown Land Macabé, 20 Jan. 1950 (fr), *Dulgeet sub MAU s.n.* (MAU); left hand side of path to Macabé plot, 20 Dec. 1965 (fr), *Forest Department sub MAU 11935 (carpol. coll. 161)* (MAU); upland forest of Macabé (fr), *Forestry Dept. sub MAU s.n.* (MAU); in plot, 6 Jan. 1967 (fl), *Vaughan sub MAU 12498* (MAU); just outside of plot, 6 Jan. 1967 (fl), *Vaughan sub MAU 12499* (MAU, 2 sheets); in plot, 18 Jan. 1976 (fr), *Vaughan sub MAU 13092* (MAU, 2 sheets); 16 Feb. 1967 (fl), *Vaughan sub MAU 13094* (MAU); corner of plot near road, 11 July 1968 (fr), *Vaughan sub MAU 13229 (carpol. coll. 187)* (MAU, 2 sheets); upland cli-

max forest of Macabé, 24 Nov. 1938 (st), *Wiehe sub MAU s.n.* (MAU). MONTAGNE COCOTTE: degraded forest, 2,200 ft. (760 m), 8 Nov. 1969 (fr), *Barclay 1693* (K); on crest, 9 Nov. 1969 (fr), *Guého sub MAU 14192* (carpol. coll. 186) (MAU); degraded forest on summit, 770 m, 1 Dec. 1978 (fl), *Lorence 1978* (MO); 4 Jan. 1979 (fl), *Lorence 2250* (K, MAU, MO, P); *Lorence 2251* (K, MAU, MO, P, REU, Z). WITHOUT PRECISE LOCALITY: 1865 (fl), *De Franqueville s.n. sub Herb. DeCandolle 16, 2: 660, no. 12* (G-DC; microfiche, MO); (fl), *Anon. sub Herb. Richard s.n.* (P); (fr), *Vaughan V 35 sub MAU spirit coll. 52* (MAU).

Tambourissa sieberi seems to be most closely related to *T. bathiei* from Madagascar, particularly in terms of floral morphology, which is discussed under the latter species. Both belong to species Group 6. Among Mauritian species, *T. sieberi* shares several features with *T. quadrifida*, including cauliflory, a thyrse inflorescence structure, closed gynoeceous floral receptacles which open by small apical pores, and similar strong, fermenting-fruity floral odors. *Tambourissa quadrifida* is totally glabrous, however, and appears to be more closely allied to the Madagascan *T. perrieri* (Group 7) than to *T. sieberi*.

A sterile collection of *Tambourissa* from northern Madagascar (*Baron 6720*, K) with similarly tomentose leaves, accompanied by a pencil sketch of a solitary, terminal fruit, apparently represents an undescribed species possibly allied to *T. sieberi*. Besides having solitary, terminal fruits, the leaves of *Baron 6720* differ from those of *T. sieberi* in containing numerous oil cells in the lamina and in having less densely branched ultimate veins. It is described as *Tambourissa* "sp. D" (no. 43) at the end of this treatment.

Flowers of *Tambourissa sieberi* are either bright yellow or dark purple, often within the same population. Floral odor in both sexes is strong and cloying, reminiscent of overripe or fermenting fruit.

Vernacular name. Bois tambour (Mauritius).

31. *Tambourissa bathiei* Cavaco, Bull. Soc. Bot. France 104: 284, fig. 1. 1957; Cavaco in Humbert, Fl. Madagascar 80: 20, fig. V:2–5. 1959. TYPE: Madagascar. Majunga: Firin-galava, right hand tributary of the Ikopa River, W of Antsiafabositra (probably July 1899) (fl), *Perrier de la Bâthie 495-A* (holotype, P).

Monoecious tree, the new growth hirsute. Leaves (known only from the inflorescence) pre-

sumably opposite, petiolate; petioles 5–6 mm by 0.8 mm, hirsutulous; lamina chartaceous, elliptic, 40–58 mm by 20–25 mm, the apex shortly acuminate, the base acutely cuneate, the secondary veins 5–7 pairs, making a 65–70° angle with the costa, the venation prominent, visible to 4° on both surfaces, the margin plane. Inflorescence cauliflorous, unisexual, a condensed pleiochasium, or thyrse of (8–)20–34 flowers, sometimes leafy, the floral axis (20–)55–95 mm long by 3–4 mm wide medially, hirsutulous-pubescent. Androeceous flower in bud globose, 10–13 mm diam., sparsely pubescent, apiculate with 3–4 minute, obtuse velutinous tepals, the pedicel 25–45 mm by 1.5–2 mm, subtended by a small, caducous ciliate deltoid bracteole 2 mm long; at anthesis deeply 3–4-fid, 25–35 mm diam., the lobes spreading $\pm$ flat; stamens numerous, ca. 350–450, clavate, 2–3 mm long by 1–1.5 mm wide, the filament well developed, comprising ca. $\frac{1}{2}$ – $\frac{2}{3}$ total length of stamen, the loculi apical, connivent or confluent at the obcordate-emarginate apex, occupying ca. $\frac{1}{3}$ – $\frac{1}{2}$ total length of stamen, the internal receptacle surface with clusters of short, dense hairs between the stamens. Submature gynoeceous inflorescence a fulvous, velutinous-pubescent condensed pleiochasium of 8 flowers, the floral axis 24 mm by 2.5 mm. Submature gynoeceous flower in bud globose, 7–8 mm diam., apiculate with 3–4 obtuse, velutinous tepals, the pedicel 12–15 mm by 1.5 mm; styles numerous, several hundred, completely lining the receptacle, narrowly conical, 1 mm long by 0.3–0.4 mm wide at the slightly ventricose base, the acuminate apex slightly papillose, the internal receptacle surface densely velutinous between the styles. Mature gynoeceous flowers, fruiting receptacle, and carpels unknown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. *Tambourissa bathiei* is known only from the type, which was collected along the Ikopa River, probably in riverine forest, in the Majunga province of western central Madagascar. The area formerly supported semideciduous dry forest of *Dalbergia* and *Commiphora*, but is now mainly savannah due to human disturbance.

On the basis of floral morphology, *Tambourissa bathiei* appears to be most closely related to *T. sieberi*, a species endemic to Mauritius, which also belongs to Group 6. Both species have small leaves, densely pubescent new growth, are cauliflorous with yellowish velutinous, generally

unisexual thyrses or pleiochasia, and globose gynoecious receptacles lined with numerous narrowly conical styles.

Although mature gynoecious flowers of *Tambourissa bathiei* are unknown, the buds are similar to those of *T. sieberi*, which open by a small, subentire apical pore only 1–2 mm diam. Androecious flowers of *T. bathiei* have numerous clavate stamens with long, distinct filaments and loculi connivent or confluent at the obcordate apex. In contrast, stamens of *T. sieberi* are broadly deltoid-ovate, sessile, and have separate lateral loculi along most of their length. Further collections, particularly mature gynoecious flowers and fruit, of this poorly known species are required. See discussion under species number 42.

32. ***Tambourissa perrieri*** Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 42. 1911; Cavaco in Humbert, Fl. Madagascar 80: 30, fig. VIII:5–7. 1959. TYPE: Madagascar. Majunga: vicinity of Maevatanana, Ampassiri, 15 July 1899 (fl), *Perrier de la Bâthie* 495 (holotype, P; isotypes, P, 2 sheets).

Monoecious shrub or tree 2–8 m tall, the bark smooth, dark, the branches spreading, the new growth sparsely pilose, glabrescent, the mature leafy stems pale green, smooth, glabrous, 2–2.5 mm diam. Leaves opposite, petiolate, glabrous; petioles 5–10(–20) mm by 1–2 mm; lamina chartaceous to subcoriaceous, both surfaces slightly lustrous, narrowly elliptic, narrowly ovate to narrowly oblong, 75–250(–280) mm by 27–50(–75) mm, the apex acuminate, the base acute to slightly obtuse, the secondary veins 7–13 pairs, making a 75–85° angle with the costa, the venation very prominent, finely reticulate, visible to 4(–5°) on both surfaces, the margin plane. Inflorescence cauliflorous on meristematic swellings on the trunk, ramiflorous or rarely terminal, a short, unisexual or sexually mixed pleiochasium of 7–9 flowers, the floral axis glabrous or with scattered hairs, 55–125 mm by 2–4 mm, each pedicel subtended by a broadly deltoid, ciliate bracteole. Androecious flower in bud globose, 9–11 mm diam., smooth, glabrous or with rare, scattered hairs, apiculate with 4 small, thick hirsutulous deltoid tepals, the pedicel 10–32 mm by 1–1.5 mm, with scattered hairs; at anthesis deeply 4-fid, 18–25 mm diam., the lobes spreading flat; stamens numerous, ca. 150–200, ovoid to obovoid or clavate, 1.8–3 mm long by 1.2–1.5 mm wide,

more or less recurved, subsessile or the filament comprising up to ½ total length of the stamen, the loculi confluent at the obtuse apex or separate, the connective retuse, not prolonged, the internal receptacle surface with scattered to clustered short, simple hairs between the stamens. Gynoecious flower in bud obovoid to obpyriform, 9–11 mm long by 6–7 mm wide, ± glabrous or with a few hairs basally, apiculate with 4–5 small, thick hirsutulous deltoid tepals, the pedicel stout, tapered, 3–15 mm by 1.5–2 mm wide medially; at anthesis obovoid to obpyriform, 12–14 mm long by 7–9 mm wide, the apex shallowly 4–5-fid, the lobes thick, erect, deltoid, the orifice 3–6 mm diam., comprising ca. ½ total width of the receptacle; styles numerous, ca. 200, crowded, shortly conical, 5-angled, 0.5–0.7 mm long by 0.5 mm diam. at the slightly ventricose base, the apex shortly acuminate, the internal receptacle surface densely velutinous with short, white hairs between the styles and on inner surface of the lobes. Fruiting receptacle solitary, borne on the trunk or branches, rarely terminal, obovoid, subglobose or rarely cupuliform, 50–150 mm long by 35–130 mm wide, externally grayish, corky, smooth or venose, the orifice comprising ⅓–½ total width of fruit, the styles conical; pedicel and peduncle 28–45 mm by 6–10 mm. Mature carpels ovoid-compressed, 8–10 mm long by 7–8 mm wide, the endocarp brown.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. *Tambourissa perrieri* appears to be commonest in the northwestern sector of Madagascar (the Diego Suarez, Sambirano and Majunga regions) where it apparently occurs in vegetation types ranging from semideciduous sclerophyllous moist forest of *Uapaca*/*Chlaenaceae* and dry forest of *Dalbergia*/*Commiphora*/*Hildegardia*, frequently along rivers, to wet forest of *Tambourissa*/*Weinmannia*. As most collections lack precise data, it is often difficult or impossible to determine the exact habitat. In addition, two collections of what appear to be *T. perrieri* (but differ in having cupuliform fruits) are known from the lower limits of the *Tambourissa*/*Weinmannia* zone (ca. 900 m) of the eastern domain at Analamazaotra near Perinet, a seemingly disjunct distribution pattern possibly attributable to undercollecting.

MADAGASCAR. DIEGO SUAREZ: Manongarvio Massif W of Sambirano River, above 510 m, Apr. 1909 (fr), *Perrier de la Bâthie* 10116 (P); Sambirano, Feb. 1923

(fr), *Perrier de la Bâthie* 15465 (P). MAJUNGA: Bemarivo River Bassin, Boina, 300 m, Aug. 1907 (fl), *Perrier de la Bâthie* 10125 (P); Mt. Bekolosy, near Maormandla, Mar. 1909 (fr), *Perrier de la Bâthie* 10117 (P). TAMATAVE: near Analamazaotra, 800 m, 1912 (st), *Perrier de la Bâthie* 10128 (P); Maromisaba, near Analamazaotra, 1,000 m, Feb. 1921 (fr), *Perrier de la Bâthie* 15958 (P).

Morphologically, *Tambourissa perrieri* most closely approaches *T. quadrifida* from Mauritius, the only other member of Group 7. Both species are cauliflorous, rarely ramiflorous or terminal, with unisexual or sexually mixed pleiochasia or thyrses produced along most of the length of the trunk. Androecious flowers of both split deeply into four flat or recurved segments bearing numerous short stamens. The gynoecious flowers of both are obovoid to obpyriform or ellipsoid with a small orifice; it is much smaller (1–2 mm diam.) in *T. quadrifida* which also has thicker, obtuse or retuse leaves with more obscure venation. Both species occur in relatively dry habitats and form a group apparently not closely allied to other members of the genus, with the possible exception of Group 6.

Vernacular name. Ambora-lavaravina (Madagascar).

33. *Tambourissa quadrifida* Sonn., Voy. Ind. Oriental ed. 1, 2: 237, tab. 134. 1782; ed. 2, 4: 405, tab. 134. 1806; Gmel., Syst. Nat. 2(1): 16. 1791; A.DC., Prodr. 16(2): 658. 1868; Baker, Fl. Mauritius 288. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901, excl. synonym. *T. obovata*; Drake in Grandidier, Hist. Phys. Madagascar 1(1): 21. 1902, pro parte, excl. synonym. *T. purpurea*, *T. rota*, *T. parvifolia*; Perk., Pflanzenr. 4, 101 (Nachtr.): 41. 1911. *Mithradatea quadrifida* (Sonn.) Comm. ex Schreb., Gen. Pl. 2: 783. 1791; Willd., Sp. Pl. 1(1): 27. 1797; Spreng., Syst. 5(3): 866. 1826. *Ambora quadrifida* (Sonn.) Poir., Encycl. 7: 565. 1806; Tabl. Encycl. 784. 1806; Tul., Monogr. Monim. 297. 1855. TYPE: Ile de France (Mauritius). Without precise locality (ca. 1775) (fl), *Commerson s.n. sub Herb. A. L. de Jussieu* 16708 [lectotype, P-JUSS, here designated (photo, MO); isoelectotypes, P-JUSS (photos, MO), both mixed with *T. elliptica* subsp. *micrantha*].

Ambora sempervirens F. G. Dietr., Lexic. Gart. 1: 342. 1802, nom. superfl., based on *T. quadrifida*.

A. tambourissa Lam. ex Steud., Nom. Bot. 37. 1821, nom. superfl., non *A. tamburissa* Boiv. ex Tul. *Mithradatea tamburissa* Bojer, Hortus Maurit. 290. 1837, nom. superfl., based on *T. quadrifida*. *Ambora neglecta* Tul., Monogr. Monim. 432. 1855. *Tambourissa neglecta* (Tul.) A.DC., Prodr. 16(2): 659. 1868; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. TYPE: Mauritius. July 1855, *Labillardiere s.n.* (lectotype, P, here designated).

Monoecious to subdioecious tree attaining 15 m tall, the stems often multiple, to 15–30 cm D.B.H., the bark light brownish gray, flaking or checking, the new growth totally glabrous, the mature leafy stems glaucous, smooth to longitudinally striate, 2–4 mm diam. (suckers to 7–8 mm diam.). Leaves opposite to subopposite (sometimes alternate on suckers), petiolate, glabrous; petioles 5–12 mm by 1–1.5 mm; lamina subcoriaceous, broadly to narrowly elliptic, oblong or obovate, (30–)45–100 mm by (13–)17–52 mm, the apex shortly acute to mucronate, obtuse, rounded or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 4–8 pairs, making a 55–65° angle with the costa, the venation ± obscure adaxially, visible to 2–3° on both surfaces, the margin plane to slightly revolute. Inflorescence a glabrous, generally ± unisexual, sometimes leafy, condensed pleiochasium or sparsely branching thyse of (3–)5–35(–110) flowers, cauliflorous on meristematic swellings along the entire length of the trunk, or the flowers rarely solitary on leafless nodes or axillary, the floral axis (30–)40–180 mm by 2–4 mm, the flowers borne singly or in cymose units of 2–3. Androecious flower in bud smooth, obovoid to ellipsoid, 10–20 mm long by 7–10 mm wide, apiculate with 3–4 minute, glabrous, obtuse-deltoid tepals, the pedicel 10–30 mm by 1–1.6 mm, occasionally jointed to a distinct peduncle up to 12 mm long, often subtended by an obtuse, ciliate bracteole 0.5 mm long by 0.5–1 mm wide; at anthesis deeply (3–)4-fid, splitting deeply to the base, 20–32 mm diam., the lobes ultimately completely reflexed; stamens numerous, ca. 300–500, ellipsoid to oblong, 1.5–2.5 mm long by 0.8–1.4 mm wide, the filament distinct, comprising ca. ¼–⅓ total length of the stamen, the connective emarginate to slightly apiculate, the internal receptacle surface with scattered clusters of short hairs between the stamens. Gynoecious flower in bud obovoid to ellipsoid, 10–16 mm long by 7–10 mm wide, smooth, glabrous, apiculate with 3–4 minute deltoid tepals,

the pedicel 7–10 mm by 1.5–2 mm, sometimes jointed to a peduncle attaining 10 mm long, often subtended by a minute bracteole; at anthesis with a subentire, shallowly 3–5-fid orifice 1–2 mm diam., the thick deltoid lobes straight or scarcely outcurved; styles numerous, ca. 200–300, lining the receptacle except near the apex, shortly conical, 0.4–0.6 mm long by 0.6 mm diam. at the abruptly swollen base, the internal receptacle surface velutinous between the styles and on the lobes, the dense hairs short, the external surface soon becoming corky. Fruiting receptacles borne on the trunk and major branches, solitary or in clusters of 2–3, irregularly obovoid-pyriform to globose-urceolate and depressed, 50–170 mm long by 50–100 mm diam., the walls 16–25 mm thick, externally corky brown, the orifice small, 5–10 mm diam., comprising ca. $\frac{1}{10}$ total width of fruit, the internal surface with numerous, scattered shortly conical styles 0.7–0.8 mm long by 0.3–0.4 mm wide basally, the pedicel and peduncle stout, 10–20 mm long by 7–18 mm diam. medially. Mature carpels ovoid-compressed, 13–19 mm long, 7–13 mm wide, 5–7 mm thick, the endocarp pale to dark brown, the surface minutely scrobiculate-rugose. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. *Tambourissa quadrifida* is restricted to the western escarpments of the central plateau, ranging from the Trois Mamelles mountain range in the north to the mountains opposite Le Morne Brabant in the south. It is local and occasional to common in evergreen or semideciduous moist forest of *Elaeodendron orientale* Jacq., *Diospyros* spp., *Mimusops petiolaris* Dubard, and other species characteristic of the relatively dry rain shadow area. Although older trees of *T. quadrifida* are still relatively common, I observed no recent regeneration of the species, possibly due to grazing pressures from the high populations of stag which are maintained in the region for hunting.

MAURITIUS. CHAMAREL: Chamarel Hill, near first hairpin bend by roadside on edge of mountain reserves, 600 ft. (ca. 200 m), 19 Apr. 1939 (fl), *Vaughan V 1512* (MAU, 5 sheets); Chamarel, Dec. 1937 (st), *Vaughan 1512A* (MAU). PITON DU FOUGE: W flank, dry forest, ca. 400 m, 9 Aug. 1975 (fl), *Lorence 1337* (K, 2 sheets; MAU); flank of mountain ridge facing Le Morne Mt. and overlooking Coteau Raffin Village, 9 Aug. 1975 (fl), *Guého sub MAU 17356* (MAU). TROIS MAMELLES MT.: dense forest near Trois Mamelles, Aug. 1928 (fl), *Vaughan 544* (K). YEMEN MATALA VALLEY: under Brise

Fer Mountain, dry forest (st), *Bernardi 14846* (G); 4 Dec. 1973 (fl), *Coode et al. 4270* (K, 2 sheets; MAU); W foothills of Brise Fer Mt., Yemen, Matala Valley, 17 Jan. 1976 (fr), *Lalouette sub MAU 17744* (MAU); 17 Mar. 1979 (fl, fr), *Lorence & Lalouette 2538* (K, MO, P, REU, Z); (fl), *Lorence & Lalouette 2539* (MO); 31 May 1979 (fl), *Lorence 2654* (K, MO, P, Z); (fl), *Lorence 2655* (K, MO, P); (fl), *Lorence 2656* (MO, REU); Yemen estate, 4 July 1968 (fl), *Maingard sub MAU 13266* (MAU); by side of road at Yemen, 4 July 1968 (fl, fr), *Vaughan sub MAU 13215* (carpol. coll. 178) (MAU, 4 sheets). WITHOUT PRECISE LOCALITY: (st), *Anon. 4663* (G, K); (fl), *Anon. sub Herb. Delessert s.n.* (G); (fl), *Anon. sub Herb. DeCandolle 16(2): 658* (G-DC, 2 sheets; microfiche, MO); (st), *Anon. sub Herb. Richard s.n.* (P, left hand collections only); *Anon. sub Herb. Richard 111* (P, 2 sheets); (fl), *Ayres s.n.* (K); (fl), *Bojer s.n.* (K); 1831 (fl), *Bouton s.n.* (P); 1814 (fl), *Carmichael s.n.* (K); (fl), *Ilardwicke 6* (G); (st), *Martin s.n.* (G); (fl), *Martin 607* (G, 2 sheets).

Tambourissa quadrifida appears to be most closely allied to *T. perrieri* from Madagascar, also of species Group 7. The latter is distinguishable by its globose androecious flower buds, gynoeceous flowers with larger orifices (3–4 mm diam.), longer, acuminate leaves with more prominent venation, and floral ground tissue with abundant oil cells lacking in *T. quadrifida*.

Living flowers produce a strong odor of ripe fruit similar to that of *Tambourissa sieberi*. Two floral color morphs occur in the population at Yemen, the androecious flowers being either tomato red or salmon orange, whereas the gynoeceous flowers have either red or greenish white to pink styles. Buds and outer receptacle surfaces are marbled green, often flushed with red.

Vernacular names. Bois tambour, Pomme de singe (Mauritius).

34. *Tambourissa alaticarpa* Lorence, nom. nov. *Phanerogonocarpus perrieri* Cavaco, Bull. Soc. Bot. France 104: 613. 1957; Cavaco in Humbert, Fl. Madagascar 80: 4. 1959 non *Tambourissa perrieri* Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902. TYPE: Madagascar. Tamatave: E coast, bank of the Fandrarazana River, 200 m, 1930 (fl), *Perrier de la Bâthie 10102* (holotype, P).

Monoecious treelet, the new growth pale yellowish villous, the hairs simple, the submature stems 3 mm diam., stramineate, villous. Leaves opposite, petiolate; petioles 15–16 mm by 2 mm, villous; lamina chartaceous, elliptic to oblong, 210–220 mm by 75–80 mm, the apex abruptly acuminate, the base cuneate, adaxially sparsely

pilose, abaxially densely pilose, the costa velutinous, depressed adaxially, prominent abaxially, the secondary veins ca. 7 pairs, making a 50–60° angle with the costa, festooned brochidodromous, the venation raised and visible to 3–4° on both surfaces, the margin serrate-dentate with 9–10 pairs of narrowly acute, antrorse teeth ca. 1 mm long, the tips glandular, indurated. Apparently cauliflorous (also ramiflorous?), the inflorescence either a sexually mixed pleiochasium 150–250 mm long with 7–10 lateral androecious flowers and a single, terminal gynoecious flower, the floral axis 100–240 mm by 1.5–3 mm, pilose to velutinous, or a short, unisexual pleiochasium 20–30 mm long of 7–10 androecious flowers, the floral axis 6–20 mm by 0.5–1 mm, pilose to villous. Androecious flower in bud glabrous or with rare, scattered hairs, obovoid to ellipsoid, 4–5 mm by 3–3.5 mm, apiculate, the apex with 3–4 acute, scarious deltoid tepals 0.5 mm long and wide, the pedicel 13–19 mm by 0.5 mm, sparsely pilose, subtended by a subulate-linear bracteole 2–3 mm long; at anthesis deeply 4-fid, 7–9 mm diam., the lobes spreading flat; stamens ca. 38, clavate, 1.2–1.6 mm long by 0.7–0.8 mm wide, the filament distinct, stout, the loculi separate, lateral or oblique, occupying $\frac{1}{4}$ – $\frac{1}{2}$ total length of the stamen, the connective obtuse or apiculate, scarcely or not prolonged, the internal receptacle surface glabrous. Gynoecious flower terminal, sparsely pilose or glabrate, in bud narrowly obovoid, tubular, 22–28 mm by 4–5 mm, angular with 4–6 longitudinal wings 1–1.5 mm wide running from apex to pedicel, the apex crowned by 6–8 subulate tepals 1–1.5 mm long, the wall ca. 0.5 mm thick, the pedicel scarcely differentiated, 20–25 mm by 1.5 mm diam. medially; at anthesis apparently opening by a small (ca. 1 mm diam.) apical orifice flanked by several deltoid lobes; styles numerous, ca. 250–300, sharply conical, 1 mm long by 0.5 mm diam. basally, acuminate, curved antrorsely, the internal apical portion of the receptacle velutinous with short, simple white hairs, the styles interspersed with short, dense hairs. Fruiting receptacle probably resembling that of *T. longicarpa* (i.e., cylindrical, narrowly winged), the fruiting carpels (fide Perrier de la Bâthie) embedded in the orange receptacular tissue, the mesocarp red, the endocarp black.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. Presumably from lowland wet for-

est of Myristicaceae/*Anthostema*, the species is known only from the type.

Along with *Tambourissa longicarpa*, *T. alaticarpa* comprises the very natural species Group 8, characterized by elongate, narrowly winged gynoecious flowers and fruits. It differs from the former species in having larger, more sparsely pubescent leaves with smaller, more numerous teeth (only 2–3 pairs in *T. longicarpa*), and externally sparsely pilose to glabrate buds and flowers.

35. ***Tambourissa longicarpa*** Lorence, nom. nov. *Phanerogonocarpus capuronii* Cavaco, Bull. Soc. Bot. France 104: 612, figs. 1–4. 1957; Cavaco in Humbert, Fl. Madagascar 80: 3, fig. I:1–6. 1959 non *Tambourissa capuronii* Cavaco, Bull. Mus. Hist. Nat. (Paris), Ser. 2, 29: 287. 1957. TYPE: Madagascar. Diego Suarez: Atondradama Pass, N of the Masoala Peninsula, E forest, ca. 500 m, 22 Dec. 1953 (fl, fr), *Capuron 8775-SF* (holotype, P).

Large monoecious treelet, the new growth pale yellowish villous, the hairs simple, the mature leafy stems fulvous velutinous, 2–3 mm diam. Leaves opposite, petiolate; petiole 10–13 mm by 1.5–2 mm, fulvous velutinous; lamina broadly elliptic, 75–105 mm by 43–65 mm, chartaceous, the apex deltoid, acute, the tip thickened, the base cuneate, the adaxial surface sparsely pilose, especially along the costa and veins, glabrescent, the abaxial surface densely pilose with pale yellowish white hairs, especially along the costa and veins, the costa depressed adaxially, prominent and rounded abaxially, the secondary veins 5–6 pairs, making a 45–55° angle with the costa, the basal pairs festooned brochidodromous, the apical ones often excurrent into the marginal teeth, the venation visible to 2° adaxially and to 3° abaxially, the margin slightly revolute, strongly dentate in the apical $\frac{1}{3}$ with (1–)2–3 pairs of broadly deltoid teeth 3–5 mm long, the tips thickened, glandular. Inflorescence basally cauliflorous, produced on meristematic swellings from the trunk, either a sexually mixed, 15–22 flowered pleiochasium with 1–3 terminal gynoecious flowers, the androecious flowers lateral in opposite to subopposite pairs or cymose groups of 2–3, the floral axis velutinous, 70–95 mm by 1–1.8 mm, subtended by several deltoid bracteoles, or a smaller unisexual pleiochasium of 7–

9 androecious flowers, the floral axis 18–35 mm by 1 mm. Androecious flower in bud hirsute, globose, 4–5 mm diam., apiculate with 1(–2) pairs of minute, subulate-deltoid tepals 0.3–0.5 mm long, the pedicel 10–22 mm by 0.5 mm, pilose, subtended by a subulate-naviculate, pilose bracteole 1 mm long; at anthesis deeply 4-fid, 9–11 mm diam., the lobes spreading flat, ultimately reflexing, each bearing 2–3 minute, fleshy tepals apically within; stamens 40–50, subulate, 1.5–2.5 mm long by 0.8–1 mm wide, the filament distinct, thick, the loculi separate, lateral or abaxially $\pm$ unifacial, 1–1.5 mm long, occupying ca. $\frac{1}{2}$ total length of stamen, the connective prolonged, acute to apiculate, the inner receptacle surface with scattered hairs between the stamens. Gynoecious flower in bud narrowly obconical, tubular, 30–35 mm by 3.5–4 mm, $\pm$ quadrangular with 4(–5) lateral longitudinal wings ca. 1 mm wide, fulvous hirsute-velutinous, the apex bearing 4–6 deltoid-subulate hirsute tepals 1–2 mm long, the receptacle wall ca. 1 mm thick, the pedicel tapered, scarcely differentiated from the receptacle, 20–25 mm by 1 mm, hirsute, subtended by 2 subulate bracteoles 2–3 mm long; at anthesis opening by 4 deltoid lobes, the orifice ca. 1 mm diam.; styles numerous, ca. 500, crowded, conical, 0.4–0.5 mm long by 0.3 mm wide basally, the base slightly ventricose, the internal receptacle surface apically velutinous, the cavity ca. 2–2.5 mm diam., the styles interspersed with numerous short hairs, a mucilaginous exudate present. Fruiting receptacle pendulous, cylindrical-ellipsoid, 160 mm by 70 mm, externally pale corky brown, bearing 4–5 longitudinal wings, 4–5 mm wide, the orifice narrow, at maturity splitting lengthwise and exposing the central tube bearing part of the carpels, the pedicel and peduncle ca. 120 mm by 6 mm. Mature carpels ovoid-compressed, 12 mm by 5–6 mm, the mesocarp thin, red-orange, fleshy, the endocarp brown, minutely foveolate.

Distribution. Endemic to Madagascar (Fig. 24).

Habitat. The type and only known collection is from the eastern lowland Myristicaceae/*Anthostema* wet forest zone.

Most closely allied to *Tambourissa alaticarpa*, the only other member of species Group 8, *T. longicarpa* differs by its smaller leaves with fewer, much larger teeth, its more densely villous inflorescence and flowers, and by its stamens with

the connective prolonged beyond the anther. Further collections and field studies are greatly desired.

- 36. *Tambourissa castri-delphinii*** Cavaco, Bull. Soc. Bot. France 104: 283. 1957; Cavaco in Humbert, Fl. Madagascar 80: 32, fig. IX:9–10 (non fig. VIII). 1959. TYPE: Madagascar. Tulear: Ebakika, Fort Dauphin district, in secondary forest (savoka), small tree, 17 Nov. 1932 (fl), *Decary 11052* (holotype, P).

Small monoecious or subdioecious trees 5–7 m tall, the mature leafy stems terete to subtriangular, 3–7 mm diam., glabrous, stramineate. Leaves ternate, rarely opposite, petiolate, glabrous; petioles 7–13 mm by 1.5–2 mm; lamina subcoriaceous, both surfaces moderately lustrous, ovate to oblong, 88–170 mm by 38–68 mm, the apex abruptly and shortly acuminate, the base acutely cuneate, the secondary veins 5–7 pairs, making a 45–50° angle with the costa, the venation raised and prominent, visible to 4° on both surfaces, the margin thickened, slightly revolute. Androecious inflorescence ramiflorous, axillary on the leafless nodes, a contracted pleiochasium or fascicle of 4–9 flowers, the floral axis 1–9 mm by 1.5–2 mm, sparsely puberulent basally, subtended by several pale, naviculate-deltoid, ciliate bracteoles 0.5–1.5 mm long. Androecious flower in bud glabrous, globose, 9–18 mm diam., apiculate with 4–6 short, obtuse tepals, the pedicel 10–18 mm by 0.8–1 mm, subtended by a bracteole; at anthesis deeply 4–5-fid, 25–32 mm diam., the lobes spreading flat, reflexing, purple within; stamens numerous, ca. 200–300, ovoid to deltoid, thin, 2.5–4 mm long by 1.5–2 mm wide, the filament short, subsessile, the loculi lateral, confluent at the obtuse apex, rarely free, the connective not prolonged, the internal receptacle surface with scattered or clustered simple hairs between the stamens. Gynoecious flowers presumably ramiflorous like the male, at anthesis napiform-depressed, 4–6 mm long by 10–14 mm diam., externally glabrous, internally densely hirtellous on the lobes, the orifice small, X-shaped, the styles numerous, ca. 800–900, conical acuminate, 0.7–0.9 mm long and wide basally, interspersed with numerous hairs; pedicel and peduncle 8 or more mm long. Mature fruiting receptacle subglobose-cupuliform, 40–45 mm long by 40–60 mm wide, externally corky, the walls 10–12 mm thick, the orifice comprising ca. $\frac{1}{4}$ – $\frac{1}{2}$ total width of fruit,

the styles conical 0.8–1.5 mm by 0.8 mm, interspersed with rare hairs; pedicel and peduncle 17 mm by 5 mm. Mature carpels ovoid-compressed, 10–11 mm by 5–8 mm, pale tan.

Distribution. Endemic to Madagascar (Fig. 30).

Habitat. *Tambourissa castri-delphinii* is known only from the SE coastal region between Mananjary and Fort Dauphin. Capuron notes that the species occurs in coastal “savoka” (secondary or disturbed primary forest) over old sand dunes.

MADAGASCAR. FIANARANTSOA: Mananjary, Mar.–Apr. 1909 (fr), *Geay* 8287 (P). TULEAR: between Fort Dauphin and Manantenina, near Manambato (fl), *Capuron* 28667-SF (P); Ebakika, 18 Nov. 1932 (fl), *Decary* s.n. (P); Mendena, 16 Feb. 1949 (fr), *Capuron* 378-SF (P); Fort Dauphin, Manambato, 12 Dec. 1972 (fl), *Jacquenim* 1197 (P).

Cavaco (1957b) states that *Tambourissa castri-delphinii* is related to *T. religiosa*, also Madagascar, because leaves of both species are similarly subcoriaceous or coriaceous with prominent venation. This similarity is most likely because both species occupy a similar habitat in coastal forest. More significantly, adult phyllotaxis is different, being opposite in *T. religiosa* and usually ternate in *T. castri-delphinii*, the latter character otherwise found only in *T. ficus* and *T. peltata*, both Mauritian endemics. In addition, venation of all three ternate-leaved species is prominent and finely reticulate, showing a high degree of organization. Furthermore, androecious flowers of *T. religiosa* and *T. castri-delphinii* are totally different. Both *T. peltata* and *T. castri-delphinii* are cauliflorous or ramiflorous on the upper branches, producing large, deeply 4(–5)-fid androecious flowers with recurved segments and numerous, broadly ovoid to deltoid subsessile stamens, whereas those of *T. religiosa* are small and globular with fewer, much smaller stamens. For these reasons *T. peltata* and *T. castri-delphinii* appear to be more closely related and I have placed them together in species Group 9.

Tambourissa peltata differs from *T. castri-delphinii* by its larger, solitary or paired androecious flowers with thicker pedicels, and discoid female receptacle with broad, sterile lobes and columnar styles. Gynoecious flowers of *T. castri-delphinii* differ from both *T. ficus* and *T. peltata* in having an X-shaped orifice.

37. *Tambourissa ficus* (Tul.) A.DC., Prodr. 16(2):

659. 1868; Perk. & Gilg, *Pflanzenr.* 4, 101: 69, fig. 18Q. 1901; Perk., *Gatt. Monim.* fig. 34Q. 1925. *Ambora ficus* Tul., *Ann. Sci. Nat. (Paris)* 4(3): 30. 1855; Tul., *Monogr. Monim.* 300. 1855. TYPE: “Java” (probably Mauritius). Without precise locality (ca. 1800) (fl), *Leschenault de la Tour* s.n. (holotype, P).

Ambora alternifolia Tul., *Ann. Sci. Nat. (Paris)* 4(3): 31. 1855; Tul., *Monogr. Monim.* 305. 1855. *Tambourissa alternifolia* (Tul.) A.DC., *Prodr.* 16(2): 660. 1868; Baill., *Adansonia*, Ser. 1, 9: 131. 1868–1870; Perk. & Gilg, *Pflanzenr.* 4, 101: 72. 1901; Cavaco, *Bull. Soc. Bot. France* 104: 284. 1957. TYPE: Ile Maurice (Mauritius). At the foot of the Pouce, above the plain at Moka, Oct. 1849, *Boivin* s.n. [lectotype, P, here designated, as to androecious floral buds only, excluding the stem and leaves which are *Homalium integrifolium* (Lam.) Baill. (Flacourtiaceae)].

Ambora obovata Tul., *Ann. Sci. Nat. (Paris)* 4(3): 31. 1855; Tul., *Monogr. Monim.* 306. 1855. *Tambourissa obovata* (Tul.) A.DC., *Prodr.* 16(2): 660. 1868; Perk. & Gilg, *Pflanzenr.* 4, 101: 70. 1901. TYPE: Ile Maurice (Mauritius). Woods of the Pouce, Sept. 1849, *Boivin* s.n. (holotype, P).

T. elliptica sensu Baker, *Fl. Mauritius* 288. 1877; sensu Perk., *Pflanzenr.* 4, 101 (Nachtr.): 44. 1911 non (Tul.) A.DC.

Ficus sapotoides Baker, *Fl. Mauritius* 284. 1877. TYPE: Mauritius. Pouce above plateau, Sept. 1862, *Ayers* s.n. (holotype, K; photo, P).

Monoecious to subdioecious treelet or tree 10–15 m tall and 10–15 cm D.B.H., the base of the trunk frequently swollen, the new growth finely pilose to fulvous tomentose, the mature leafy stems glabrous, stramineate, subterete, 2–5 mm diam. Leaves ternate to subalternate, rarely opposite to subopposite, petiolate, glabrous; petioles 10–25 mm by 1.5–2 mm (to 45 mm long on vigorous suckers); lamina chartaceous to subcoriaceous, broadly to narrowly obovate, oblanceolate, narrowly to broadly elliptic, 60–150 (–180) mm by (20–)30–75 mm (to 170 mm by 100 mm on vigorous suckers), the apex acuminate, acute, obtuse or retuse, the base acutely decurrent to acutely cuneate, the secondary veins 5–8(–11) pairs, making a 50–70° angle with the costa, the venation finely reticulate, prominent, visible to 3–4° adaxially and to 4° abaxially, the margin plane to slightly revolute; juvenile and sucker leaves often heterophyllous, the petioles red when living, the lamina apically serrate-dentate with 1–3 pairs of teeth. Inflorescence cauliflorous on the swollen base of the trunk, sometimes extending up the lower portion of the trunk for several meters or rarely on the leafless parts

of the lower branches, the flowers solitary or in fascicles of 2(–3) on the meristematic swellings. Androecious flower in bud globose-depressed to napiform-depressed, 20–30 mm diam. by 15–25 mm long, pubescent, smooth to corky, longitudinally ribbed basally, the walls thick and fleshy, apiculate with 3–5 minute, hirsute tepals, the pedicel stout, tapered, jointed near the base, the pedicel and peduncle 15–25 mm by 3–4.5 mm diam. medially, pubescent to velutinous, bearing several hirsute, subulate-naviculate bracteoles 1–2 mm long; at anthesis shallowly to deeply 4–6(–7)-fid, either partially closed and urceolate, 20–40 mm diam. by 17–30 mm long, or the lobes spreading flat open, 35–75 mm diam.; stamens very numerous, ca. 900–1,800, curvate, linear to ellipsoid or ligulate, 3–6 mm long by 0.5–1 mm wide, the filament basally thickened, comprising $\frac{1}{4}$ – $\frac{1}{3}$ total length of the stamen, the loculi separate, parallel, lateral, or abaxially $\pm$ unilateral and extrorse, comprising ca. $\frac{1}{3}$ total length of the stamen, the connective thick, apically prolonged, obtuse to apiculate or acute, comprising ca. $\frac{1}{4}$ – $\frac{1}{3}$ total length of the stamen, the internal receptacle surface with clusters of simple hairs between the stamens. Gynoecious flower in bud napiform-depressed, thick, fleshy, the size and pubescence as in the androecious bud; at anthesis urceolate-napiform, 30–40 mm diam. by 15–30 mm long, externally corky brown, sparsely puberulent, the orifice ca. 15–25 mm diam., comprising ca. $\frac{2}{3}$ total width of the receptacle, the 6–8 thick, deltoid lobes incurved; styles very numerous, ca. 1,000–2,000, narrowly conical or setose, 1.5–5 mm long by 0.3–0.5 mm wide basally, the sides longitudinally furrowed, the internal receptacle surface densely velutinous between the styles. Fruiting receptacle solitary at the base of the trunk, irregularly cupuliform, often $\pm$ compressed dorsally, 40–85 mm long, 135–175 mm wide, the orifice subentire, 90–130 mm wide, comprising ca. $\frac{2}{3}$ – $\frac{3}{4}$ total width of the receptacle, the walls 10–16 mm thick, both surfaces corky brown, internally with numerous, setose styles 1.5–4.5 mm long by 0.5–0.8 mm wide basally, the pedicel and peduncle 20–65 mm long by 9–10 mm diam. medially. Mature carpels ovoid-compressed, 10–14 mm long, 5–7 mm wide, 4–6 mm thick, the endocarp dark brown, the surface scrobiculate.

Distribution. Endemic to Mauritius (Fig. 38).

Habitat. *Tambourissa ficus* is fairly widespread in mid to upper elevation wet and cloud

forest formations (ca. 600–800 m), often forming localized populations near the summits of mountains or along rivers and lakes.

MAURITIUS. BAMBOU MOUNTAIN: top of Bambou Mt., 7 Oct. 1962 (fl), *Mulnier sub MAU s.n.* (MAU). BASSIN BLANC: forest inside Bassin Blanc Crater, 4 Nov. 1967 (fl), *Guého sub MAU 13228* (MAU); lower montane rain forest inside crater, 550 m, 21 Dec. 1978 (fr), *Lorence 2188* (K, MAU); (fl), *Lorence 2189* (MO); (fl, fr), *Lorence 2190* (MO); ca. 2 m from outside of lake, S side, 500 m, 25 May 1976 (fr), *Richardson et al. 4164* (K, MAU, MO); indigenous forest, 13 Mar. 1971 (fr), *Staub sub MAU 19283* (MAU). BRISE FER: 200–300 yards before summit of Piton Brise Fer, 29 Dec. 1966 (fl), *Guého sub MAU 12505* (MAU, 2 sheets); (fl), *Guého sub MAU 12509* (MAU); Brise Fer Mt., 609 m, July 1960 (fr), *Lalouette sub MAU 10020* (carpol. coll. 111) (MAU, 2 sheets); 20 Aug. 1966 (fr), *Lalouette sub MAU 12194* (carpol. coll. 158) (MAU); mature evergreen forest transitional to dry forest, 600 m, 8 Dec. 1978 (fl), *Lorence 2114* (MO); (fl), *Lorence 2115* (MAU, MO); (st), *Lorence 2116* (MO); (st), *Lorence 2117* (MO); a few hundred yards before reaching the summit of Brise Fer, 1 Oct. 1964 (fr), *Vaughan sub MAU 11429* (carpol. coll. 154) (MAU); (st), *Vaughan sub MAU 11430* (MAU); (fl), *Vaughan sub MAU 12505* (spirit coll. 167) (MAU). CROWN LAND DANGUET: near Port Louis, 4 Sept. 1947 (st), *Vaughan V 3177* (MAU). MACABÉ FOREST: ravines of Black River Gorges near Macabé, 28 Nov. 1950 (fl), *Duljeet FD 105* (spirit coll. 41) (MAU, 2 sheets); Macabé forest, near kiosk, transitional wet forest, ca. 660 m, 16 Dec. 1978 (st), *Lorence 2155* (MAU); (st), *Lorence 2156* (MO); Plateau Colophane below Macabé, ca. 600 m, 15 Jan. 1979 (st), *Lorence 2952* (MO); Macabé, near screen, 10 Dec. 1938 (st), *Vaughan sub MAU 1336A* (MAU); Macabé forest transect, 11 Aug. 1937 (st), *Vaughan 27 sub MAU 2359* (MAU); Macabé climax forest near large “natte” tree in plot, 16 Nov. 1967 (fl), *Vaughan sub MAU 13055* (MAU). MT. COCOTTE: degraded forest, 2,200 ft. (ca. 760 m), 8 Nov. 1969 (fl), *Barclay 1692* (K); dense indigenous thicket along crest, 8 Nov. 1969 (fl), *Guého sub MAU 14108* (MAU); low cloud forest with *Nuxia*, invaded by exotics, N slope, ca. 700 m, 19 Dec. 1978 (fl), *Lorence & Lecordier 2162* (K, MO); near summit, 770 m, 19 Dec. 1978 (fl), *Lorence & Lecordier 2163* (MO, P); forest of St. Marie near Mt. Cocotte, high forest, Nov. 1937 (fl), *Wiehe sub MAU 1511* (spirit coll. 45) (MAU). MT DEUX MAMELLES: degraded wet forest invaded by exotics, 630 m, 22 Jan. 1979 (st), *Lorence 2303* (MO). MT LAGRAVE: low forest on slopes, much invaded, 5 Apr. 1974 (fr), *Coode 5034 sub MAU 17598* (K, MAU). PIETER BOTH MT. RANGE: S flank below “La Fenêtre,” totally degraded wet forest, ca. 550 m, 29 Sept. 1978 (st), *Lorence 1833* (MO). PITON DU MILIEU: dense indigenous thicket, rocky ridge at foot of the mountain, 25 Oct. 1969 (fl), *Guého sub MAU 14181* (MAU); low native thicket halfway up steep summit, 24 Nov. 1971 (fl), *Guého sub MAU 14983* (MAU); degraded lower montane wet forest, 650–750 m, 29 Dec. 1978 (st), *Lorence 2235* (MO); (st), *Lorence 2236* (MO). PITON DU FOUGE: E slopes, ca. 500 m, 27 Apr. 1976 (st), *Richardson et al. 4042* (K). POUCE MT.: shoulder of Le Pouce, Dec. 1860 (fl), *Ayres s.n.* (K);

shoulder of Le Pouce, Nov. 1862 (fl), *Ayres s.n.* (K); (st), *Boivin s.n.* (P, mixed with *T. pedicellata*); lower montane wet forest invaded by exotics, grading into cloud forest near summit, 600–700 m, 14 Dec. 1978 (st), *Lorence 2142* (MO); (fl), *Lorence 2143* (MO); 750–800 m (fl), *Lorence 2144* (K, MAU). RIVIÈRE DES GALETS: below Cascade 500 Pieds, 350 m, forest along river bank, 8 Nov. 1975 (fl), *Lorence 1485* (K, 2 sheets; MAU); Valley of Cascade 500 Pieds, *Calophyllum* wet forest, 550 m, 22 Dec. 1978 (st), *Lorence 2193* (MO). TAMARIN FALLS RESERVES: 518 m (fl), *Vaughan sub MAU 1509* (MAU). VUILLEMAN FOREST: near Midlands (fl), *King sub MAU 1765* (MAU). WITHOUT PRECISE LOCALITY: (fl), *Anon. sub Herb. Richard s.n.* (P, 2 sheets); common in forests of medium altitude (st), *Vaughan sub MAU 1513* (MAU).

Although one of the most polymorphic Mauritian species, *Tambourissa ficus* is nevertheless distinct from all other Mascarene species, and is the only one with flowers and fruit produced on the swollen base of the trunk. It is potentially monoecious [e.g., *Wiehe 1511* (MAU), *Vaughan sub MAU 12505* (MAU), *Lorence 2162* (MAU, MO)] but frequently produces flowers of a single sex. Although only four to eight flowers are produced during a single season per plant, this paucity has been compensated for by a floral gigantism unrivalled in the genus and indeed the entire family! Fully expanded androecious flowers may attain 60–75 mm diam. with the entire surface covered by ca. 900–1,800 stamens, whereas gynoecious flowers are large, urceolate cups 30–40 mm diam. lined with a comparable number of styles. The cupuliform fruits, which attain 175 mm diam., are also some of the largest in the genus.

Both foliar and floral morphology are variable in *Tambourissa ficus*, but are relatively constant within a given population. For example, populations from the central (Le Pouce Mt., Piton du Milieu) and western (Piton Brise Fer) mountain ranges have broadly elliptic to obovate, acute to obtuse leaves, hence the specific epithet *obovata* given by Tulasne. Those from the southern edge of the central plateau (Bassin Blanc, Mt. Cocotte, Rivière des Galets) tend to have narrower, elliptic to oblanceolate, acute to acuminate leaves. Such variation may occur within a single population, however, e.g., at Macabé forest.

Variation in floral morphology is expressed in length of stamens and styles, and form and color of androecious flowers. Populations from Bassin Blanc and Rivière des Galets, which grow along river and lake banks, have shorter styles and creamy white, urceolate androecious flowers that tend to split only about halfway open. Popula-

tions from mountain summits (e.g., Le Pouce and Piton Brise Fer) have pinkish to reddish purple androecious flowers that split completely open into a star shape and the gynoecious flowers have longer styles. Flower color and size and shape of stamens and styles are similarly variable in other species, e.g., *T. tau* and *T. quadrifida*. These floral and foliar differences intergrade gradually in *T. ficus*, making it impossible to formally recognize infraspecific taxa. For example, the Bassin Blanc population has androecious flowers and styles that are transitional between the Rivière des Galets and Brise Fer forms. As such, they are best recognized as variants of a single, polymorphic species.

In view of this variation, it is not surprising that *Tambourissa ficus* has been described as three distinct species of *Ambora* by Tulasne (1855a). He based *A. obovata* on a single sterile, leafy twig from Le Pouce and based *A. alternifolia* on a mixed collection consisting of androecious buds of *T. ficus* and leaves of *Homalium* (Flacourtiaceae). Furthermore, because the type of *A. ficus* consists of leaves and gynoecious flowers of the narrow-leaved form, which moreover was supposed to have been collected in Java, it is understandable that Tulasne described it as another species. He was apparently unaware that J. Leschenault de la Tour first visited Mauritius, where he apparently collected the type of *A. ficus*, before continuing on to Java (Steenis-Kruseman, 1950). *Tambourissa* is unknown from Java, and the locality on the label is evidently erroneous (Perkins, 1911).

I have lectotypified *Tambourissa alternifolia* on the basis of the large, solitary ficiform androecious flower buds with characteristic ligulate, apiculate stamens obviously belonging to *T. ficus*. I recognize the leaves as belonging to a Mascarene species of Flacourtiaceae [*Homalium integrifolium* (Lam.) Baill.] also occurring on Le Pouce Mt. Its leafy stem is minutely lenticellate, unlike any *Tambourissa* known to me, and furthermore the leaves lack the oil cells characteristic of Monimiaceae (Perkins & Gilg, 1901), a fact ignored by Cavaco (1957b).

Baker (1877) wrongly referred material of *Tambourissa ficus* from Le Pouce to *T. elliptica*. More surprisingly, he described comparable material of the same species, also from Le Pouce, as *Ficus sapotoides*, suggesting he failed to dissect flower buds and also overlooked the absence of stipule scars on the stem. Of the three available concurrently published names, I have retained

T. ficus because the type is the most complete, with both androecious and gynoecious flowers and leaves.

Tambourissa ficus belongs to the small species Group 9, also including *T. peltata* (Mauritius) and *T. castri-delphinii* (Madagascar). The ternate to subalternate leaf condition of these species appears to be derived, as seedlings and suckers of *T. ficus* and *T. peltata* have opposite leaves. *Tambourissa ficus* is most closely allied to *T. peltata* in leaf morphology but its leaves are thinner and generally lack the bright yellow-green tinge characteristic of *T. peltata*, and the stems are more slender. In addition, *T. ficus* is monoecious, usually basally cauliflorous, and has much larger flowers with more numerous parts. Furthermore, its gynoecious flowers are urceolate with setose styles as opposed to those of *T. peltata*, which are flat and discoid with columnar styles and produce a thick, mucilaginous exudate. With respect to gynoecious floral morphology, *T. ficus* more closely approaches Group 5, thus linking the two groups.

Vernacular names. Bois tambour, Pot de chambre jacot (Mauritius).

38. *Tambourissa peltata* R. Br. ex Baker, Fl. Mauritius 288. 1877; Perk. & Gilg, Pflanzenr. 4, 101: 71. 1901. TYPE: Mauritius. Without precise locality, 1814, *Carmichael s.n.* (lectotype, K, here designated, as to gynoecious collection only).

Dioecious treelet or tree 12–15 m tall and 30–40 cm D.B.H., the outer bark smooth, pale brown, longitudinally fissured, the new growth glabrous, the mature leafy stems smooth, stramineate, 3–7 mm diam., angled or subterete. Adult leaves ternate to subalternate, petiolate, glabrous; petiole 12–25 mm by 1–2 mm; lamina subcoriaceous to coriaceous, broadly to narrowly obovate, oblanceolate, elliptic, broadly elliptic or rarely ovate, 60–150(–180) mm by 30–70(–85) mm (reaching 225 mm long on vigorous suckers), the apex acuminate to acute, frequently obtuse or retuse, the base acutely cuneate to acutely decurrent, the secondary veins 6–9(–12) pairs, making a 55–65° angle with the costa, the venation very prominent and finely reticulate, visible to 4° on both surfaces, the margin slightly revolute; seedling and sucker leaves opposite, heterophyllous, the petiole red when living, the lamina oblanceolate to narrowly oblanceolate, with 1–3 pairs of short teeth apically. Inflores-

cence ramiflorous on the leafless branches or upper portions of the trunk, rarely axillary or on short, leafy shoots, the flowers solitary or in fascicles of 2–3. Androecious flower in bud glabrous, globose to ellipsoid, 10–14 mm diam. by 12–18 mm long, apiculate with 5–6 small, acute glabrous tepals, the pedicel and peduncle 6–20 mm by 1.5–3 mm, bearing few to many deltoid-naviculate, ciliate bracteoles to 1.5 mm long; at anthesis deeply 4–6(–7)-fid, 30–50 mm diam., the thick lobes ultimately reflexing; stamens numerous, ca. 200–400, ovoid-deltoid to linear-lanceolate, 4–7 mm long by 1.5–3 mm wide, the filament short or subsessile, the loculi separate or confluent apically, occupying almost entire length of the stamen, the connective broad, slightly prolonged or not, the internal receptacle surface glabrous, rarely with scattered hairs. Gynoecious flower in bud glabrous, broadly napiform-depressed, 14–17 mm diam. by 7–9 mm long, apiculate with 4 minute tepals, the pedicel and peduncle 6–12 mm by 2 mm, bracteolate as in androecious flower; at anthesis deeply 4–7-fid, 23–30 mm diam., the deltoid lobes ultimately reflexing, their internal surface $\pm$ verrucose-wrinkled, the receptacle discoid, flat to $\pm$ concave, the peltate central portion 13–16 mm diam., pubescent around the margin and between the styles; styles numerous, ca. 400–500, crowded and coalescent, virtually indistinguishable, columnar, 4–6-sided, 0.3–0.5 mm long by 0.3–0.4 mm diam., the apex flat to depressed, the gynoecium covered with a mucilaginous exudate. Fruiting receptacle solitary on the old stems or rarely on the upper part of the trunk, sometimes produced in large numbers, cupuliform, patelliform or discoid-peltate, 40–130 mm diam. by 15–60 mm long, externally corky brown or mottled, the walls 8–20 mm thick, the orifice broad, subentire, comprising $\frac{3}{4}$ or more of the total width of the receptacle, the internal receptacle surface corky brown, with numerous short, bluntly columnar 4–6-sided styles 0.5–1 mm diam. by 0.5 mm long, often subtended by clusters of hairs, the pedicel and peduncle stout, 10–25 mm long by 6–20 mm diam. Mature carpels ovoid-compressed, 9–13 mm long, 4–8 mm wide, 3–6 mm thick, the endocarp dark brown, lustrous, the surface scrobiculate. Gametic chromosome number, $n = 19$.

Distribution. Endemic to Mauritius (Fig. 40).

Habitat. The commonest and most widely distributed species of *Tambourissa* in Mauritius,

T. peltata displays a wide ecological amplitude, ranging from lowland wet forest (e.g., at Bel Ombre, ca. 300 m, annual precipitation 2,400 mm), to upland evergreen moist forest (e.g., Mt. Corps de Garde, 750 m, annual precipitation 1,600 mm), or cloud forest (e.g., Mt. Cocotte, 760 m, annual precipitation 5,000 mm). Locally abundant in some areas, it may become a sub-canopy or canopy tree (e.g., at Macabé high forest), or remain a stunted treelet (e.g., at Pétrin in *Philippia* heath formation).

MAURITIUS. BAMBOU MOUNTAIN RANGE: crest between Mt. Camisard and Piton Bambou, 28 July 1971 (fl), *Guého sub MAU 15052* (MAU). BASSIN BLANC CRATER: rain forest with *Calophyllum*, 550 m, 21 Dec. 1978 (st), *Lorence 2187* (MO). BEL OMBRE: June 1977 (fl), *Friedmann 3151* (P); wet forest with Sapotaceae, ca. 200–400 m, 27 Dec. 1978 (st), *Lorence 2213* (MO); (st), *Lorence 2214* (MO). BRISE FER MT.: Nov. 1960 (fr), *Lalouette 3008 sub MAU 10003* (carpol. coll. 101) (MAU). BELLE RIVE: (fr), *H. Rouillard s.n.* (MAU). CASCADE ALEXANDRA: S edge of central plateau, low, stunted wet forest, ca. 650 m, 25 Mar. 1979 (fl), *Lorence 2552* (MO). CHAMAREL HILL: top of hill, 1,100 ft. (ca. 350 m), 31 Jan. 1940 (fr), *Vaughan sub MAU 1912* (MAU, 2 sheets). CORPS DE GARDE MT.: summit ridge, ± stunted forest, ca. 750 m, 15 Nov. 1973 (fr), *Coode et al. 4064* (K, MAU). CROWN LAND RIVIÈRE: on bank along pipe to water tower, 30 July 1964 (fr), *Vaughan sub MAU 11009* (MAU). CUREPIPE: Forestry Department nursery, along stream bank with remnants of indigenous trees, ca. 700 m, 15 Dec. 1978 (fr), *Lorence 2151* (MAU, MO); 14 Mar. 1971 (fr), *Remy sub MAU 15489* (MAU). GAULETTES SERRÉES: north-central Mauritius, low mixed wet forest over lava, ca. 400–450 m, 19 May 1979 (fl), *Lorence et al. 2642* (K, MO); (fl, fr), *Lorence et al. 2643* (K, MO, P). LION MT.: by side of path leading to summit, along crest, 22 Mar. 1976 (fr), *Lalouette sub MAU 17878* (MAU). MACABÉ FOREST: Macabé to Brise Fer road, low mixed evergreen forest over laterite, ca. 660 m, 8 Dec. 1978 (fr), *Lorence 2101* (MAU, MO); Macabé forest, near kiosk, transitional wet forest, ca. 660 m, 16 Dec. 1978 (st), *Lorence 2154* (MO); Macabé forest, ca. 700 m, 7 Feb. 1975 (fr), *Lorence sub Coode 4791* (K, MAU); near path leading to Macabé via the marshes, 14 Feb. 1963 (fr), *Vaughan sub MAU 10682* (MAU, 2 sheets). MARE LONGUE PLATEAU: Mare Longue-Macabé road, on right bank of river flowing into Mare Longue reservoir, 10 Mar. 1967 (fl), *Guého sub MAU 12543* (MAU, 2 sheets); low, mixed wet forest along stream, ca. 700 m, 10 Apr. 1979 (fl), *Lorence 2586* (K, MAU, MO); 14 Apr. 1979 (fl), *Lorence 2593* (MO); near new reservoir, 1,900 ft. (ca. 600 m), 11 May 1946 (fr), *Vaughan V 3139* (carpol. coll. 6) (MAU, 2 sheets). MONTAGNE DES CRÉOLES: E Mauritius, transitional evergreen forest, ca. 250–300 m, 25 Jan. 1979 (st), *Lorence & Julien 2338* (MAU, MO); (fr), *Lorence & Julien 2339* (MAU, MO); (fr), *Lorence & Julien 2340* (MO); (fr), *Lorence & Julien 2341* (MO, P). PERRIER NATURE RESERVE: near Mare aux Vacoas, low mixed wet forest, ca. 600 m, 27 Mar. 1979 (fl), *Lorence 2555* (MO); 9 Apr. 1979 (fl), *Lorence*

2585 (K, MO); 23 Apr. 1976 (fr), *Richardson et al. 4009* (K, MAU); (fr), *Richardson et al. 4010* (K); near quadrat by small stream, Dec. 1937 (fl), *Vaughan sub MAU 1437* (MAU, 2 sheets); (fl), *Vaughan sub MAU 1438* (MAU); 15 June 1939 (fl), *Vaughan sub MAU 1534* (MAU); 6 June 1969 (fl), *Vaughan sub MAU 13774* (MAU, 2 sheets); in dense indigenous thicket, 14 May 1970 (fl), *Vaughan sub MAU 14184* (MAU); (fl), *Vaughan sub MAU 14185* (MAU, 2 sheets); 22 Apr. 1970 (fl), *Vaughan sub MAU 14193* (MAU, 2 sheets); by stream, 9 Oct. 1975 (fr), *Vaughan sub MAU 17543* (MAU). PÉTRIN NATURE RESERVE: *Philippia* heath formation over laterite, 630 m, 4 Apr. 1979 (fl), *Lorence 2572* (MO, P). PIETER BOTH MT.: S flank below La Fenêtre, very degraded wet forest invaded by exotics, ca. 400 m, 23 Jan. 1979 (st), *Lorence 2319* (MAU, MO). PLAINE CHAMPAGNE: road to Plaine Champagne, dense indigenous thicket, 21 July 1966 (fr), *Guého sub MAU 12232* (MAU, 2 sheets); SE of triangulation point, low heath formation of *Philippia* and *Helichrysum* over laterite, ca. 700 m (fr), *Lorence 2197* (MAU, MO). POUCE MT.: Le Pouce Mt. plateau, mixed wet forest invaded by exotics, grading into cloud forest near summit, 600–700 m, 14 Dec. 1978 (fr), *Lorence 2146* (K, MO); 14 Feb. 1979 (fr), *Lorence 2402* (B, K, MAU, MO, P, REU, Z). SEPT CASCADES: (fr), *Hardy s.n.* (MAU). TAMARIN RIVER: river reserves near Tamarin River Bridge, at Mare aux Vacoas, 2 June 1966 (fl), *Vaughan sub MAU 12168* (MAU, 2 sheets); 5 May 1966 (fl), *Vaughan sub MAU 12240* (MAU, 2 sheets). VACOAS RIDGES: 21 Jan. 1968 (fr), *Guého sub MAU 13077* (carpol. coll. 175) (MAU). WITHOUT PRECISE LOCALITY: (fr), *Anon. sub MAU 11004* (carpol. coll. 159) (MAU); (fl), *Anon. 3132* (G); (st), *Bojer sub MAU 1312* (MAU); (fl), *Carmichael s.n.* (K, syntype); (st), *Carmichael s.n.* (K); (fr), *Remy s.n.* (MAU); 16 Aug. 1962 (fr), *Tilbrook sub MAU 10548* (MAU); 3 Sept. 1962 (fr), *d'Unienville sub MAU 10624* (MAU); 30 Mar. 1964 (fl), *d'Unienville sub MAU 11206* (MAU, 2 sheets).

Leaf shape in *Tambourissa peltata* is relatively variable, a character which tends to remain constant within populations. Populations from the eastern mountain ranges (e.g., Montagne des Créoles, Mt. de Lion, and Mt. Bambous) are characterized by narrowly elliptic to oblanceolate leaves, whereas most populations from the upland plateau have the usual obovate leaves. Fruit morphology ranges from typically cupuliform to flat and discoid, both extremes occasionally on the same tree (e.g., *Lorence 2151*). Androecious flower size and color are variable within populations but remain constant on a given tree. Dark purple-red androecious flowers are most common, whereas the salmon pink ones are less frequent. Gynoecious flower color is less variable, the central disc being reddish orange and the sterile lobes dull purple-red and verrucose. At anthesis, the disc secretes a copious thick, clear mucilage which covers the styles and is probably functional in pollination (see Endress,

1979, 1980b). Flowers of both sexes produce strong, sour odors of fermenting fruit or tomatoes.

Tambourissa peltata belongs to the small species Group 9, whose members are characterized by ternate to subalternate leaves, also including *T. ficus* (Mauritius) and *T. castridelphinii* (Madagascar). *Tambourissa peltata* strongly resembles and is apparently closely related to the latter species; both are ramiflorous with similar androecious flowers and stamens, and have leaves with prominent, finely reticulate venation. *Tambourissa peltata* differs by its larger, solitary or fasciculate androecious flowers and is the only species known to have flat, discoid gynoecious flowers with star-like sterile lobes. Flowers of *T. ficus* are much larger than those of the preceding species and are produced at the swollen base of the trunk. The only other dioecious species in Mauritius, *T. cordifolia*, does not seem to be closely related to *T. peltata*, but rather belongs to species Group 5, although the two are known to hybridize naturally at Pétrin.

Vernacular name. Bois tambour (Mauritius).

IMPERFECTLY KNOWN SPECIES

39. *Tambourissa lastelliana* (Baill.) Drake in Grandidier, Hist. Phys. Madagascar 1(1): 24. 1902; Perk., Pflanzenr. 4, 101 (Nachtr.): 44. 1911. *Monimia lastelliana* Baill., Bull. Mens. Soc. Linn. Paris 1: 342. 1882; Perk. & Gilg, Pflanzenr. 4, 101: 65. 1901. TYPE: Madagascar. Without precise locality, 1841, *de Lastelle s.n.* (holotype, P).

Dioecious (?) shrub or tree (?), the mature leafy stem glabrous, 4 mm diam., longitudinally striate-pustular, the rays relatively narrow, the nodes dilated, with multiple axillary buds, the internode 80 mm long. Leaves opposite, petiolate; petiole recurved, 15 mm by 2 mm, glabrescent; lamina thickly chartaceous, brown, adaxially glabrescent, abaxially with scattered simple, straight to slightly curved simple hairs 0.5 mm long, denser and longer (to 1–1.5 mm) along the major veins and costa, the lamina broadly obovate-cuneate, $\pm$ involute, the apex shortly acuminate, the base cuneate, the apical portion of the lamina with 4–5 pairs of broad, deltoid teeth 1.5–4 mm long, the tips indurated, the venation mixed, basally festooned brochidodromous, apically craspedodromous, the secondary veins excurrent into

the marginal teeth, ca. 5 pairs, making a 35–40° angle with the costa, the venation strongly depressed adaxially and visible to 3°, raised abaxially and visible to 4°, the margin revolute. Androecious inflorescence ramiflorous (?), presumably a dichasium or the flowers solitary, the floral axis pilose-tomentose basally, fulvous, ca. 10 mm by 1.5 mm or longer, subtended by several obtuse-deltoid tomentose bracteoles. Submature androecious flower in bud 6–7 mm diam., globose, densely golden pilose externally, the apex slightly depressed, with several minute tepals, the pedicel ca. 5 mm by 1 mm, golden pilose; stamens ca. 60–70 per flower, in bud ca. 3–4 mm long by 1 mm wide, the loculi lateral, separate, occupying the medial $\frac{2}{3}$ of the stamen, laterally dehiscent, the filament short, the connective prolonged, acute, the internal receptacle surface with scattered simple hairs between the stamens; tanniferous idioblasts and oil cells present in the receptacle wall.

Distribution. Presumably endemic to Madagascar. The type is said to be from eastern Madagascar (Baillon, 1882), presumably from low or mid altitude evergreen wet forest.

The type of *Monimia lastelliana* consists of a single, detached leaf, a leafless twig, and several detached androecious flower buds. Unlike *Monimia*, which has entire leaves with festooned brochidodromous venation and predominantly or uniquely stellate trichomes, the leaf of *de Lastelle s.n.* has dentate margins in the apical portion, mixed craspedodromous and brochidodromous venation, and bears only simple trichomes as do the flower buds. Furthermore, stamens of *de Lastelle s.n.* lack the paired basal appendages characteristic of *Monimia* and have instead long, laterally dehiscent loculi and an acutely prolonged connective, all lacking in *Monimia* as noted by Perkins (1911). The pollen is too immature to permit diagnosis. Nevertheless, it is clear that *de Lastelle s.n.* does not represent a species of *Monimia*, nor even belong in the subfamily Monimioideae (sensu Thorne, 1974), and was correctly removed from the genus by Drake del Castillo (1902).

Its eglandular stamens with laterally dehiscent loculi, and long, uniquely simple trichomes instead suggest placement in the subfamily Molinedioideae (sensu Thorne, 1974) with the other Madagascan genera. The globose buds with minute, reduced tepals most closely recall those of

Tambourissa. Although venation is festooned brochidodromous in most *Tambourissa* species, that of *T. longicarpa* and *T. thouvenotii* is basally brochidodromous and tends to become craspedodromous in the toothed apical portion of the lamina, much as in *de Lastelle s.n.* On the basis of androecious floral morphology and leaf structure, it is most probable that *de Lastelle s.n.* actually does represent a species of *Tambourissa* as proposed by Drake del Castillo (1902).

40. *Tambourissa* sp. A.

Habit unknown. Leaves opposite, petiolate; petiole 17–24 mm long; lamina chartaceous, elliptic, 80–100 mm by 34–43 mm, the apex acuminate, the base cuneate, the venation visible to 5–6° on both surfaces. Androecious inflorescence (cauliflorous?) a dichasium, the elongate floral axis ca. 130 mm long; the androecious flower in bud cylindrical, obovoid-ellipsoid, ca. 12–15 mm long, apiculate, the pedicel 7 mm by 1 mm; at anthesis splitting deeply into 3 segments; stamens numerous, ligulate, ca. 2 mm long, the loculi confluent apically, occupying nearly the entire length of the stamen; flowers red when living. Gynoecious flowers, gynoecious inflorescence, and fruit unknown.

MADAGASCAR. TAMATAVE: Iaroka, Maroantsetra, 1,000 m, 20 June 1968 (fl), *Rakotozafy 847 bis* (MAD).

The elongate androecious buds most closely resemble those of *Tambourissa quadrifida* from Mauritius. It probably represents an undescribed species from the mid altitude *Tambourissa/Weinmannia* wet forest zone.

41. *Tambourissa* sp. B.

These collections have opposite leaves, the petiole to 23 mm long; lamina coriaceous, obovate, to 85 mm by 48 mm, the apex obtuse, emarginate, the base cuneate, the margin revolute. Immature androecious flower buds rami-florous on leafless nodes, solitary, the pedicel ca. 20 mm long, the bud 7–8 mm diam., the stamens with lateral loculi and a prolonged connective.

MADAGASCAR. FIANARANTSOA: Ampamaherana, 14 Dec. 1949 (fl), *Anon. sub SF-1252* (MAD, P).

The species resembles *Tambourissa crassa* from Réunion in leaf, but in the latter species the flowers are larger and always terminal, and the connectives are not prolonged. This collection probably represents an undescribed species for which I could not find the precise locality on any map.

42. *Tambourissa* sp. C.

Tambourissa amplifolia sensu Cavaco in Humbert, Fl. Madagascar 80: 34. 1959 non (Bojer ex Tul.) A.DC.

Tree to 5 m, the leaves large, the petiole 10–16 mm long, the lamina ovate-elliptic, 140–180 mm by 60–80 mm, shortly acuminate apically, rounded basally, the secondary veins 4–7 pairs. Unlike *Tambourissa amplifolia* (Mauritius), the petioles, costa, and veins are densely hirtellous abaxially.

MADAGASCAR. FIANARANTSOA: Farafangana, Befotaka, 17 Aug. 1926 (st), *Decary 5040* (MAD, P); NE Madagascar, without precise locality (st), *Thiny s.n. in 1904* (P).

These collections either represent an undescribed species from the lowland wet forest zone in the northeast and east, or may be referable to *T. decaryana*, for which only inflorescence leaves are known.

43. *Tambourissa* sp. D.

Habit unknown. Leafy stems pale brown, velutinous, 1.5–2 mm diam., the new growth velutinous. Leaves opposite, petiolate; petioles 5–10 mm by 1 mm, velutinous; lamina subcoriaceous, adaxially glabrescent, abaxially pubescent, especially along the costa and major veins, ovate-elliptic, the apex acute to shortly acuminate, the base acutely cuneate, slightly decurrent, the secondary veins 4–6 pairs, making a 55–60° angle with the costa, the venation visible to 2(–3°) adaxially, to 4° abaxially, the margin entire, revolute. Flowers unknown. Fruiting receptacle (fide Baron's pencil sketch of 6720, K) terminal, subglobose, ca. 45–55 mm diam., the orifice subcircular, subentire, comprising ca. 1/4–1/3 total width of the fruit. Mature carpels unknown.

MADAGASCAR. N Madagascar (probably DIEGO SUAREZ): without precise locality, ca. 1882 (st), *Baron 6720* (K; see also Baron's sketch of a fruit with the specimen).

Distribution. Presumably endemic to Madagascar.

The collection consists of two sterile leafy branches plus Baron's pencil sketch of the fruit. The leaves are similar to those of *Tambourissa sieberi* (Mauritius), but differ in having numerous oil cells dispersed throughout the laminar tissue and in having less highly branched venation (only to 4°), nor does *T. sieberi* ever have solitary, terminal fruits. It probably represents an undescribed species.

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down the gena to the bottom of the head. Middle of face with no pile. The occiput is tumid in the middle behind and bears quite long, fine, somewhat bristly pile, which is rather loose and scattered. It is more prominent in females. The eye is large and in females may be somewhat rectangular. In other females and in males it may be approximately hemispherical and bare. Postmargin of eye plane. The proboscis is short, stout, compressed laterally, with short, stout labellum. It is very little longer than the head or even shorter. Palpus slender but nearly as long as the proboscis. It bears fine, scattered hairs. The front is small in males, flat, pollinose, and without pile. In females, however, it bears numerous, long, fine, scattered, erect, bristly hairs and is slightly inflated or raised.

The antennae are attached just a little above the middle of the head and are characteristic. The first segment is elongate to a varying extent, as long or even longer than the next 2 segments and is extraordinarily swollen, stout and robust. It is cylindrical in form with abundant, long, fine, bristly hairs, more abundant below and lacking only on the medial surface. The second segment is barely longer than wide, much more narrow and likewise bears similar long bristles, more abundant below. The third segment in the type-species is much reduced, knob-shaped at the base, very slender, still more so on the outer half, slightly spindle-shaped, expanded at the tip and bears a tiny, spine-tipped microsegment. In other species it is wider, but similar. In some species at least laterally it is nearly as wide as the second segment, narrowed only near the apex.

Head, anterior aspect: The head is not quite as wide as the thorax, the eyes are rounded medially and are in contact for only a short distance. The antennae are adjacent in some species, but very narrowly separated in the type-species. The ocellar tubercle is minute, the ocelli quite tiny lying in an equilateral triangle. The tubercle bears a few long, fine, erect hairs. The oral opening is large and wide, extending almost to the antennae in some species. The genae are also quite wide and the oragenal cup, while comparatively deep in the middle and behind, extends outwardly only as a narrow, low, creased rim, usually not showing from the side. Genal pile loose but long and extensive. The tentorial fissure is a mere line. From the dorsal aspect the occiput meets medially in a shallow groove below the vertical column.

Thorax: The thorax is short and broad, slightly humped, rather more so in the type-species, and subopaque black. The type-species is quite opaque. Whole surface covered with two kinds of pile, short, glittering, curled, subappressed pile in many species, especially the type-species, in others with very fine, pale, more or less erect hairs, and all species in addition have a considerable amount of fine, long, erect, bristly hairs. Bristles absent. Scutellum rather thin, the vestiture like that of the mesonotum. Mesopleuron with moderately dense, long, pale pile and sometimes with additional, fine, black, bristly hairs. Pteropleuron and

hypopleuron bare, metapleuron with a conspicuous vertical brush of long, coarse pile in front of the halteres. There is also a tuft of hairs behind the spiracle. Metapleural pile may be present or absent. Squama with a wide fringe of long pile.

Legs: The legs are rather short and relatively stout. Anterior tibia with minute, fine, bristly spicules in 2 rows posteriorly. Middle tibia with much longer, spiny bristles in 4 rows with 4 or 5 in each row. Hind tibia similar with 10 to 12 bristles in each row. There are no bristles or spines beneath the femora but there are a few, scattered, long, fine hairs ventrally beneath all 3 pairs of femora. Pile of legs flat-appressed, rather shaggy in Nearctic species, more scalelike and more appressed in the type-species. Pulvilli long and spatulate, claws small and fine and sharp.

Wings: The wings are rather slender in most species, the costa sometimes with spiny tubercles in the males. There are 3 submarginal cells, all posterior cells and anal cell widely open, the discal cell is rather long, the anterior crossvein lies near or just beyond the basal third of this cell. The wings are hyaline or sometimes show a mottled brown pattern. Marginal cell gradually widened apically; at its end the vein turns up abruptly and is either rounded or plane, but in species with 2 submarginal cells it is bulbous at apex. Axillary lobe narrow, the alula likewise. Ambient vein complete. The base of costa has a weakly developed comb. Costal hook not present.

Abdomen: The abdomen is unusually broad and flattened, varying from short oval to elongate oval. It is much wider than the thorax, in most species it has abundant, short, curled, glittering, appressed pile and in addition over flat surface of the abdomen numerous long, scattered, erect hairs, which are very slender and fine but stiffer in the type-species. While usually the abdomen is opaque or nearly so, some species have the abdomen very shiny without the appressed pile, and without lateral tufts. Many species, including the type-species, have odd, dense tufts of pile along the sides of the abdomen, long at the base of a tergite and shorter toward the end. Terminalia small, recessed, the dististyli visible from below in the male. Sternites with long, dense pile.

The male terminalia from dorsal aspect, epandrium removed, show a short, compact, broad body. The epiphallus is short, and quite wide basally with slender, triangular or conical apex. The dististyli are long, elongated, and pointed apically. From the lateral aspect they are hooked upward and backward; they are also convergent. The epandrium is large and subquad-rangular.

Material studied: I have before me both sexes of the type-species and four Nearctic species from the Western States, and I have seen additional species in the collections of the National Museum of Natural History.

Immature stages: The hosts are unknown but Priddy

(1939, 1958) recalls finding a pupal skin that had emerged from soil. See comments under life histories.

Ecology and behavior of adults: Adults are attracted to spring flowers where I have taken them in the New Mexico desert. Van Duzee (1931) records an extraordinary abundance of a species of *Conophorus* Meigen on flowers along the Salinas River, California.

Distribution: Nearctic: *Conophorus amabilis* (Osten Sacken), 1877 (as *Ploas*); *atratus* (Loew), 1872 (as *Ploas*); *auratus* Priddy, 1954; *chinooki* Priddy, 1954; *collini* Priddy, 1958; *columbiensis* Priddy, 1954; *cristatus* Painter, 1940; *fallax* (Greene), 1921 (as *Calopelta*); *fenestratus* (Osten Sacken), 1877 (as *Ploas*); *hiltoni* Priddy, 1958; *limbatus* (Loew), 1869 (as *Ploas*); *melanocercatus* Bigot, 1892; *nigripennis* (Loew), 1872 (as *Ploas*); *obesus* (Loew), 1872 (as *Ploas*); *painteri* Priddy, 1958; *pictipennis* (Macquart), 1840 (as *Ploas*); *rufulus* (Osten Sacken), 1877 (as *Ploas*); *sackenii* Johnson and Maughan, 1953; *serratus* (Coquillett), 1894 (as *Ploas*).

Palearctic: *Conophorus aduncus* (Loew), 1870 (as *Ploas*), male only; *aegyptiacus* Bezzi, 1925; *alpicola* (Villeneuve), 1904 (as *Ploas*); *antennatus* Paramonov, 1940; *asiaticus* Paramonov, 1929; *bellus* (Becker), 1906 (as *Ploas*); *bivittatus* (Loew), 1862 (as *Ploas*); *bombyliiformis* (Loew), 1873 (as *Ploas*) [= *aduncus* (Loew), 1870 (as *Ploas*), female only]; *caucasicus*, Zaitsev, 1960; *chinesis* Paramonov, 1929; *chlorizans* (Rondani), 1873 (as *Codionus*); *decipiens* (Loew), 1873 (as *Ploas*); *engelii* Paramonov, 1947 [= *decipiens* Engel, 1934, not Loew]; *flavescens* (Meigen), 1820 (as *Ploas*); [= *hamillkar* Paramonov, 1929]; *fuliginosus* (Wiedemann in Meigen), 1820 (as *Ploas*) [= *atratus* Meigen, 1830]; *fuminervis* (Dufour), 1852 (as *Ploas*); *fuscipennis* (Macquart), 1840 (as *Ploas*); [= *fumi-pennis* Schiner, 1862]; *glaucescens* (Loew), 1863 (as *Ploas*); *greeni* Austen, 1936; *griseus* (Fabricius), 1787 (as *Bombylius*) [= *ater* (Lamarck), 1816 (as *Ploas*), = *atratus* (Meigen), 1820 (as *Ploas*), = *hannibal* Paramonov, 1929]; *heteropilosus* Timon-David, 1952; *hindlei* Paramonov, 1931; *kozlovi* Paramonov, 1940; *loewi* Paramonov, 1929; *luctuosus* (Loew), 1870 (as *Ploas*); *lusitanicus* (Guérin-Méneville), 1835 (as *Ploas*); *mauritanicus* Bigot, 1892; *monticola* Paramonov, 1929; *nobilis* (Loew), 1873 (as *Ploas*), *nobilis iranicus* Paramonov, 1940; *paraduncus* Paramonov, 1929; *pictipennis* (Macquart), 1840 (as *Ploas*) [= *macroglossa* (Dufour), 1852, (as *Ploas*)]; *pseudaduncus* Paramonov, 1929; *pusillus* (Loew), 1869 (as *Ploas*); *rjabovi* Paramonov, 1929; *rossicus* Paramonov, 1929; *simplex* Loew, 1869 [= *similis* Kertész, 1909, lapsus]; *syriacus* Paramonov, 1929; *talyshensis* Zaitsev, 1960; *turkestanicus* Paramonov, 1929; *ussuriensis* Paramonov, 1940; *validus* (Loew), 1869 (as *Ploas*); *virescens* (Fabricius), 1787 (as *Bombylius*); [= *hirticornis* Latreille, 1804, = *latus* (?Dufour in Vernal), 1909 (as *Ploas*), = *luridus* (Wiedemann in Meigen), 1820 (as *Ploas*), = *mourus* (Mikan), 1796 (as *Bombylius*)].

Genus *Conophorina* Becker

FIGURES 33, 269, 481

Conophorina Becker, Ent. Mitt., vol. 9, p. 181, 1920. Type of genus: *Conophorina bicellaris* Becker, 1920, by monotypy.

Small flies with the general form of *Conophorus* Meigen, but with a different type of antenna and with only 2 submarginal cells. The face and gena are more prominent, likewise more hairy. The scanty, scattered, long, erect hairs on the postmargins of the tergites, upon the mesonotum, occiput above, vertex, sides of face and basal antennal segments are very characteristic. The pile is even longer and more abundant in males. Also the pile in part in females is differently colored from males, the hair of the face and antenna being golden rather than brownish black.

The eyes in the male are extensively holoptic; the front is reduced and small although equilateral and it bears a few, long, golden, flattened hairs on each side. Genitalia protruded, but relatively small and inconspicuous, surrounded by only a few, sparse, bristly hairs.

The venation is quite simple and generalized. The first two antennal segments are thickened through their middles, but much less so than in *Conophorus* Meigen; both segments are elongate and hairy, and segment two is almost as long as the first. The palpus is distinctly 3 segmented, which is unusual.

This genus is based upon a single South African species.

Length: 4 to 5 mm.

Head, lateral aspect: Head hemispherical, the occiput short with pile which is long and erect, abundant but not dense. Just below the middle of the eye the bristly pile becomes shorter, appressed, and directed outward toward the eye margin. The front is broad, rather flattened, but with the ocellar tubercle exceptionally large with the area in front of it swollen, leaving the middle of the front below, sunken. The ocellar triangle obtuse. Pile at vertex between the ocelli consists of 4 or 5 very long, slender, bristly hairs. There is a tuft of other equally long hairs at each eye corner and curled forward. Sides of front and middle of front above antenna with numerous appressed or subappressed, golden, scaliform hairs. The front in the male is very small, triangular, pollinose, without pile, and the small but steep ocellar tubercle has an extensive tuft of long, erect, bristly hairs. The face is moderately produced forward beneath the antenna, a distance certainly not more than half the length of the first antennal segment, and vertically it is rather short, much encroached upon by the large oral recess. The pile of the face consists of a conspicuous, sublateral fringe of numerous, coarse, golden, bristly hairs. On the upper part this fringe mingles with the equally long, golden bristly hairs of the first two antennal segments. The fringe continues shorter and a little more sparse, down the sides of the gena to the bottom of the head. The eye is large,

slightly wider below, the upper facets much enlarged in the male.

Proboscis elongate, rather stout, about twice the length of the head, extending a little beyond the very long antenna. The palpi are rather large, long, flattened and pointed, a little more than half as long as the proboscis and with a few oblique setae laterally and apically. Palpus with 2 segments. The antenna is attached a little above the middle of the head, the first segment is stout, a little swollen, 3 or 4 times as long as wide, with dense, long bristly pile on all sides. The second segment is equally stout, elongate barrel-shaped, about $2\frac{1}{2}$ times as long as wide and also with considerable long bristly pile. The pile of the head and antenna in the male is chiefly, almost entirely black. In the female, almost entirely golden. The third antennal segment is more slender, a little longer than the first segment, with a distinct knob at the base, widened beyond, strongly flattened, and narrowed beyond the middle. It has a small, short, attenuate microsegment, bearing a spinous bristle apically.

Head, anterior aspect: From the front the head is wider than the thorax, not quite twice as wide as high. The eyes of the male are in contact for a long distance, leaving the male front a small equilateral triangle. Also, the ocellar triangle is small but high, and the anterior ocellus rests upon the eye margin. In the female the eyes are widely separated by almost a third the width of the head. The ocellar tubercle is much larger, rather abruptly elevated, and there is a sunken depression in the middle of the front. The antennae are narrowly separated. The oral cup is large, short oval, comparatively deep posteriorly, slanting outward anteriorly with narrowly separated pubescent ridges anteriorly. Margin of cup especially on the posterior half linearly thin and extending only a short distance forward from the very wide gena, between which there is a linear crease.

Thorax: Short and broad and rather strongly convex both in front and behind with a large, wide, thick, posteriorly convex scutellum. The mesonotum is largely opaque black with traces of shining vittae anteriorly. The postalar callosity and scutellum are polished and shining. The pile is comparatively scanty, semi-appressed or flat-appressed and consisting of golden scaliform pile in both sexes. It is apt to be denuded over the central part of the mesonotum, but a little better preserved and a little more abundant on the notopleuron, and postalar callosity lying above the wing, in front of the scutellum, and on the margin of the scutellum. In addition to this appressed, golden scalcation there are scattered, very long, erect, slender, blackish hairs in length equal to those found upon the post-vertex or upon the abdomen. They are distributed loosely and scantily over the mesonotum and scutellum, except where they are denuded. Mesopleuron with a large tuft of long scaliform golden pile. Pteropleuron,

metapleuron, and hypopleuron bare. Fringe of squamae long and forming a comparatively thick brush. Halteres large, and the large knob rather flattened, and the whole dark sepia.

Legs: Moderately stout, but the femora are not swollen. All 3 pairs have a loose fringe of long, stiff hairs ventrally, perhaps bristly hairs. In addition they are covered with long, flat-appressed, golden scales or scale-like hairs. Anterior tibiae and tarsi with numerous, oblique, short, stout spicules or spinous setae below, and 4 or 5 tiny, slender bristles above on the tibia. Middle tibia with 3 or 4 slender, oblique bristles below, the same number a little more stout above. Hind tibia with 7 slightly longer, slender, oblique, curved bristles anterodorsally and 12 or 15 shorter ones posterodorsally, but with only 2 or 3 ventrally. Claws stout, short, rather blunt, with long, slender, spatulate pulvilli.

Wings: Slender, nearly hyaline, tinged by comparatively dense, brown villi. Only 2 submarginal cells, the second submarginal cell is long and relatively narrow. The anterior crossvein enters the discal cell at the outer third. The anterior intercalary vein is rectangular, plane, and not quite as long as the anterior crossvein. The first posterior cell is of uniform width throughout. The anal cell is rather widely open. The second anal vein curved distally. Axillary lobe narrow. Alula absent. Ambient vein complete and the marginal fringe long. The third vein arises from the second vein rather than the converse, and it does so well before the end of the second basal cell. Costal comb absent.

Abdomen: About $1\frac{1}{2}$ times as long as the thorax. At the base as wide as the thorax and then rather strongly tapered, conical, and pointed apically in the female. The seventh tergite forms an equilateral triangle, but it is shorter and transverse in the male. The abdomen is largely opaque black with small, polished, shining areas laterally. The pile forms a tangled mat of partly flat-appressed and partly erect, golden, scaliform pile, in which, however, there are a number of scattered, very long, erect, quite slender, black, bristly hairs, which are very readily denuded. Females with the last sternite yawning backward and downward, but the terminalia within recessed and enclosed by a fringe of hair. Male terminalia protrusive, the hypopygium turned sidewise. Hesse (1938) states that the basimeres are not narrowed in the neck region and that the beaked distimeres are elongate and narrow, the aedeagus with a ventral process below and the lateral struts short.

Material available for study: A male of the type-species and other material in the British Museum (Natural History). Also, material kindly sent by Dr. A. J. Hesse for dissection and study.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Conophorina bicellaris* Becker, 1920.

Genus *Aldrichia* Coquillett

FIGURES 65, 285, 482, 495

Aldrichia Coquillett, Trans. American Ent. Soc. Philadelphia, vol. 21, p. 93, 1894a. Type of genus: *Aldrichia chrmanii* Coquillett, 1894, by monotypy.

These Nearctic flies are approximately the same size range as *Conophorus* Meigen but are more slender. The pile is relatively fine and erect and true bristles are lacking. There are 3 submarginal cells but the venation differs in several particulars. The marginal cell is of uniform width meeting the costa at a right angle with a rounded apex; the first submarginal cell likewise is not expanded, is relatively long, and is rectangular at the base where the posterior branch of the third vein forms a crossvein. The wing is likewise uniquely different in the form origin of the second vein which arises rectangularly, sometimes with a backward spur, close to the anterior crossvein.

Aldrichia Coquillett differs from *Conophorus* Meigen in the form and character of all three antennal segments. The first segment is shorter and in fact not quite as long as the second segment, both quite hairy above and below, and the short third segment is flattened and oval with 3 small microsegments and bristly apical spine.

Length: 9 to 11 cm.

Head, lateral aspect: The head is globular, the occiput prominent in females, less so in males, the face is scarcely visible in the lateral aspect and the oragenal cup not at all. The vertical depth of the face is less than the thickness of the second antennal segment at its apex. The face is pollinose and bare. The pile of the occiput consists of numerous, though not dense, bristly hairs which are much longer in the female and in both sexes are much longer medially than laterally, except for 2 or 3 hairs near the eye margin. The eye is large, hemispherical, the posterior margin entire. Proboscis short, very stout, with large, flared, four-lobed labellum, fleshy and muscoidlike. The whole length of the proboscis no longer than the eyes. Palpus consists of 1 very long, rather stout, outwardly curved, apically rounded segment almost as long as the eye, which bears numerous long, fine hairs on all sides, except medially. The front in females is a little inflated and bears a number of quite long, slender, bristly, erect hairs, as long as those of the vertex, among which are a few short, glittering, curled, subappressed hairs. Male front minute, flat, pollinose, without pile, forming an equilateral triangle and without a groove. Antennae attached at the head; they are quite large and conspicuous, actually a little longer than the head, the first 2 segments both strongly swollen and robust though not as much swollen as in *Conophorus* Meigen. These first 2 segments are approximately equal in length and each contain much moderately long, shaggy, or somewhat bristly pile on all sides except medially and medial pile is present apically on the second segment. Third segment large,

flattened, quite wide, except at the immediate apex, including the small, spine-tipped microsegment. The third segment nearly or quite as long as the second segment.

Head, anterior aspect: The head is not quite as wide as the thorax and not quite twice as wide as high. The front widens slightly toward the antennae, and there is a transverse groove shortly in front of the antennae. In the male the eyes are in contact for a distance of nearly 3 times the length of the front, and eyes bulge upward from the point of contact. The antennae are narrowly separated, the ocellar tubercle small, prominent, the ocelli forming an acute triangle in the male, and equilateral triangle in the female and the tubercle bears 10 or more long, slender, bristly hairs. The oral opening is large, though shallow, its walls narrow and thin. The genae are moderately wide, recessed inward from the eye margin down to a linear tentorial fissure. Viewed from above both males and females are shallowly bilobate.

Thorax: The thorax is elongate, slightly convex, opaque black and covered loosely with fine, erect, rather short pile, and about the same amount of fine, short, appressed, curled, glittering pile. The pile is much more abundant in the female than in male. Humerus with a tuft of comparatively dense, coarse, rather long, shining pile. Scutellum shining with curled, glittering pile on the disc, and disc and margin with numerous, fine, long, erect, stiff hairs, more numerous in the female, and the curled hair seemingly absent in the male. Notopleuron with 3 or 4 long, slender, black bristles. Pleuron sparsely pollinose, largely bare, the posterior border and the upper border of the mesopleuron with long, loose, abundant, coarse pile. Remainder of pleuron bare, except for a tuft of hairs behind the spiracle. Squamal fringe wide but rather short.

Legs: The legs are comparatively short and the femora a trifle thickened. Anterior tibia with 6 short, fine bristles or spicules posterodorsally. Middle and hind tibiae with 4 rows of longer, but slender, bristles, 5 or 6 in each row. Femora ventrally with a few scattered short hairs, the pile appressed and somewhat scaliform though not conspicuously so. Claws short, sharp, strongly curved, pulvilli long and broad.

Wings: The wings are slender, tinged with brown, all cells widely open, 3 submarginal cells, first submarginal cell curved forward to meet the costa just before the tip of the wing. Marginal cell very little widened apically. The medial crossvein or intercalary vein long and quite rectangular. Anterior crossvein lies a little before the middle of the discal cell. The second vein arises curiously and characteristically as a rectangular crossvein just before the anterior crossvein and it has a short backward spur. Axillary lobe quite narrow, the alula also quite narrow. Costal comb weak.

Abdomen: The abdomen is comparatively elongate, at the base as wide or a little wider than the thorax and loosely covered with flattened, curly, appressed, glittering, brassy pile, which is more abundant in the fe-

male; and in addition, sparse, erect, black, bristly hairs along the postmargin of the tergites. Sides of the first and the curled undermargin of all of the tergites with numerous, long, erect, brassy-white pile. Females with 7 tergites, males with 9 tergites. Last sternite in the female more or less triangular forming a down-turned flap and with a tuft of bristly hairs at the apex and concealing on each side a row of dense, brassy pile, which in turn conceals the female terminalia. In the male the dististyli lie side by side, only visible from below.

Material available for study: I have before me a pair of the type-species presented to me by Dr. R. H. Painter, and I have seen other material in museums.

Immature stages: Unknown.

Ecology and behavior of adults: The adults are taken on low-growing flowers in the North Central States of America, south of the Great Lakes. Painter (1939, 1940) records them from flowers of *Amorpha* sp., from *Thaspium barbinode*, and also from dewberry.

Distribution: Nearctic: *Aldrichia auripuncta* Painter, 1939; *ehrmanni* Coquillett, 1894.

Genus *Prorachthes* Loew

FIGURES 115A, 259, 479, 494, 1012, 1013, 1014

Prorachthes Loew, Berliner Ent. Zeitschr., vol. 12, p. 381, 1868.

Type of genus: *Prorachthes ledcreri* Loew, 1868, by monotypy.

Dumontiella Séguy, Encycl. Ent., ser. B, II, vol. 6, p. 162, 1932.

Type of genus: *Dumontiella vespertilio* Séguy, 1932, by monotypy.

Cheilohadrus Hesse, Ann. South African Mus., vol. 34, p. 674, 1938. Type of genus: *Cheilohadrus conspersipennis* Hesse, 1938, by original designation. Subgenus of *Prorachthes* Loew.

Paramonov (1931a), p. 104, key to 6 Palaearctic species.

Engel (1932), pp. 49-50, key to 6 species, after Paramonov.

Small blackish flies that are peculiar because of the diffuse, curiously marbled or mottled patterns of whitish spots on the wings which characterize all of the known species. There are 2 submarginal cells; the first posterior cell is open maximally and discal cell is triangular with the anterior crossvein lying beyond the middle. Marginal cell expanded apically with the end of the cell broadly rounded. The pattern of spots varies in the different species; the wing presents an effect superficially like a species of *Haematopota* Meigen. The alula is virtually absent.

The face is extraordinarily tumid and swollen, the occiput rather swollen also. The antennae are stout, and within Palaearctic species the third segment is conspicuously and characteristically flattened, dilated, and widened and nearly as broad as long. The occiput, thorax, and abdomen bear rather dense, flattened, shining scales.

The genus is not closely related to others, but with the expanded occiput, shortened proboscis, and bristly, in-

flated antennal segments, I believe it shows some relationship to the Conophorini.

This genus is restricted to the Palaearctic, especially the Transcaucasus area from which or near which most species are known. One subgenus, *Cheilohadrus* Hesse, is known from South Africa, differing markedly in the form of the antennae, which is only slenderly spindle-shaped with dorsal spinules.

Length: 4.5 mm. to 7 mm.; wing the same length.

Head, lateral aspect: The head is subglobular but largely because of the tumid face and swollen occiput. Posterior eye margin both plane and entire. The lower half of the front is separated from the upper, comparatively flattened portion by a transverse, shallow depression. The lower part of the front bearing the antenna is almost if not quite as produced and tumid as the face. The face is produced, but recedes only below and opposite the proboscis. The oragenal cup is in evidence only medial to the deep, rounded, punctate depression opposite the proboscis. The face bears dense, erect, moderately long, black bristles. Pile of the front similar but more sparse and shorter. The occiput is tumid and bears scattered, shining, metallic scales along the sides and a little hair only ventrally between the lower eye corner with some additional hairs near the upper eye margin. Palpus quite short, the base very slender, the apical portion gradually and clavately widened with the apex truncate. Proboscis short, little greater in length than the head but extending as far as the antenna. It is markedly flattened laterally and quite narrow from the dorsoventral aspect. The antenna is large and conspicuous, the first segment is robust, twice as wide at apex and bears numerous long setae, stout and more conspicuous along the apical margin. The second segment is only about one-fourth or one-fifth as long as the first segment and much reduced in width. The third segment in Palaearctic species is greatly widened and dilated dorsoventrally and sharply and rather abruptly reduced in size at the apex.

Head, anterior aspect: The head is very little wider than high but with the genofacial space very extensive and occupying more than half the total width. The genae occupy two-thirds of this space. Oral opening short oval. Eyes of the male usually holoptic for some distance, the upper facets a little enlarged. In some species, the eyes of the male are narrowly separated. The eyes of the female are widely separated. The antennae lie adjacent to one another. The ocelli are large, set on a low tubercle and are equilaterally placed.

Thorax: The thorax is about as long as wide and slightly narrowed anteriorly. The head is wider than the anterior thorax but more narrow than the posterior thorax. Mesonotum dull black, or dark colored with scattered, shining, metallic, and rather broad scales over the surface, together with a few minute, appressed setae which are more in evidence on the sides of the notopleuron. There are especially dense patches of scales on each side in front of the scutellum, and above the wing, and likewise on the sides of the scutellum. The

disc of the scutellum bears a number of not very long, erect, black setae or bristly hairs. Pleuron largely bare, except for a few scales and setae in the upper corner of the mesopleuron. Metapleuron with a tuft of rather dense, erect, bristly, black pile and posterior hypopleuron with a similar shorter tuft.

Legs: The legs are comparatively short; all the femora are slightly thickened through the middle and bear minute, flat-appressed, scaliform pile. The anterior femur below has a few quite short, fine, erect setae. Claws fine, long, and sharp with short pulvilli about half as long as the claws. Arolium minute, short, and conical.

Wings: The wings are rather large and elongate with an opaque whitish pattern greatly modified by slaty or sooty blackish color in a characteristic mottled or marbled pattern for each species. The wing is slightly narrowed basally, the axillary cell narrowed toward the base and the alula, except in *conspersipennis* Hesse, quite narrow but with a fringe of a few long hairs. There are 2 submarginal cells; the marginal cell is greatly widened apically, the 4 posterior cells are widely open, the anal cell also widely open. Discal cell rather short, much widened distally, the medial crossvein but little longer than the upper intercalary vein, and the anterior crossvein enters the discal cell at the outer third or even beyond. Ambient vein complete.

Abdomen: The abdomen is short oval but broad at the base and a little wider than the thorax; it is rather shining dark brown or blackish and bears rather numerous, short, wide, appressed, metallic scales. Posterior margins of tergites with a few fine, erect, coarse, or bristly hairs. Basal portions of the tergites sometimes tend to have foveate depressions. For *conspersipennis* Hesse, that author notes that the "basimere of the male has bristly hairs, the distimeres (beaked apical joints) are elongate, taper to a point, provided with dense, bristly, short hairs, not depressed above, but hollowed out below; aedeagus without a ventral process, its dorsum not produced on either side; lateral struts broad and leaf-like."

Material available for study: The series of this genus in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Engel (1933) records taking *beckeri* Paramonov upon flowers of a *Euphorbia* species. Paramonov found his examples on the border of a woods.

Distribution: Palaearctic: *Prorachthes beckeri* Paramonov, 1926; *lederi* Loew, 1868; *longirostris* Bezzi, 1925 [= *crassipalpis* Villeneuve, 1930, = *vespertilio* (Séguy), 1932 (as *Dumontiella*); *pleskei* Paramonov, 1926; *portschinskyi* Paramonov, 1926; *stackelbergi* Paramonov, 1926; *vespertilio* (Séguy), 1932 (as *Dumontiella*).

Ethiopian: *Prorachthes conspersipennis* (Hesse), 1938 (as *Cheilohadrus*), *conspersipennis aereophilus* (Hesse), 1938 (as *Cheilohadrus*).

Genus *Legnotomyia* Bezzi

FIGURES 31, 254, 255, 469, 474, 800, 801, 802

Legnotus Loew, Neue Beiträge III, p. 41, 1855. Type of genus: *Legnotus trichorhocus* Loew, 1855, by original designation, as no. 80 in Loew's collection as *Bombylius trichorhocus* Loew. Preoccupied by Schödté, Hemiptera, 1848.

Legnotomyia Bezzi, Zeitschr. syst. Hymen. und Dipt. Teschen-dorf, vol. 2, p. 191, 1902. Change of name.

Legnotus Bischof, Wiener Ent. Zeitung, vol. 22, p. 42, 1903.

Psiatholastus Becker, Zeitschr. syst. Hymen. und Dipt., vol. 6, p. 145, 1906. Type of genus: *Psiatholastus bombyliiformis* Becker, 1906, by original designation.

Engel (1932), pp. 58-59, key to 4 Palaearctic species.

Odd, medium-size flies; the head, legs, and thorax shining black, the abdomen dull, feebly shining black. The abdomen is very broad, short, and rounded, considerably wider than the thorax and but little convex. The postmargins of the tergites are opaque, creamy yellow, the dorsal pile quite sparse, fine, long, and erect; pile on the sides and apex of abdomen more abundant, and stiffer, and all of the pile golden yellow; sides of tergites turned under laterally. The wing may be tinged with brown in the middle, brown on the basal half, or with a middle cross band; it is wide apically, but the axillary lobe is much narrowed and the alula is narrow. Marginal cell bulbous and sometimes greatly expanded backward at its apex. First posterior cell open maximally; anal cell widely open. Anterior crossvein quite variable; it is situated at the middle, or just beyond the middle of the discal cell. In *Legnotomyia cineracea* Austen it lies before the basal third and the discal cell is short, wide, angulate below. In addition to the above peculiarities the antennae are unique. The first segment is short, about twice as long as wide; the second segment is very short; the third segment is elongate, angularly expanded below in the middle or swollen over the whole basal half and narrowed apically. At the apex it bears 4 or 5 long, distinctive, yellow bristles. Face with a few long hairs; gena and oral cup bare. Proboscis long; occiput swollen, especially below. *Legnotomyia* Bezzi has 4 posterior cells, 2 submarginal cells. It is a somewhat aberrant member of the Bombyliinae. I cannot see the slightest basis for placing *Legnotomyia* Bezzi in the Usinae, which subfamily has 3 posterior cells, closed and stalked anal cell, eliminated face, and other distinctions.

Legnotomyia Bezzi is restricted to the Palaearctic with the exception of one species from South Africa. *Psiatholastus* Becker is Palaearctic.

Length: 5 mm. to 9 mm.

Head, lateral aspect: Head globular, the face and oragenal cup rather extensive and well developed. The occiput prominent, even in males, but gradually sloping to the eye margins. Face densely micropubescent and also with about 20 long, shining, coarse or flattened hairs extended forward on each side of the face. Pile of occiput rather scanty laterally and shorter, becoming longer, coarse and somewhat more abundant medially.

The eye is hemicircular, the posterior margin entire, but also the posterior border of the eye extending or bulging outward from the occiput. Proboscis very long and slender, at least 4 times as long as the head. The labellum is slender, short, and cylindrical. Palpus relatively short, slender with 2 or 3 relatively long, apical, bristly hairs, and the basal segment quite short. Front in the male flattened and pollinose with a few, long, scaleform hairs appressed forward. Antennae attached at the upper sixth of the head; they are relatively short; the first segment is a little over twice as wide, more than twice as long as the very short second segment, which is only half as long as high. Both first and second segments have a pronounced dorsal, medial spur. Third segment rather wide in the middle and somewhat flattened, a little narrowed at base and apex, which segment bears a small, bicolored microsegment at the apex and this segment characteristically bears 8 or 10 short bristles dorsally and laterally in the middle, 4 or 5 longer bristles below in the middle, and 5 equally long at the apex. The first segment bears some moderately long, stiff hairs dorsolaterally, and a few below in the middle.

Head, anterior aspect: The head is about $1\frac{1}{2}$ times wider than high, distinctly oval, the front in the male comparatively large and triangular, the eyes in the male almost but not quite touching for a short distance, the upper facets enlarged. The ocellar tubercle is comparatively large and protuberant, the large ocelli lie adjacent to the eye in a short isosceles triangle, the oral opening is quite large, short rectangular and quite deep in the middle and behind; its walls are thin, the gena is relatively sharp and narrow and more or less sharply and rectangularly separated from the oragenal cup, the outer walls of which are polished and bare; the tentorial fissure is narrow, but deep opposite the proboscis. From above, the postvertex is not at all bilobate and the central cavity of the occiput is small.

Thorax: The thorax is short, wide, gently convex, shining black, covered with loose, scattered, erect, fine hairs of moderate length and little denser anteriorly. There is a tuft of similar hair in the upper posterior corner of the mesopleuron which extends outward, a fringe along its upper border which extends upward. The scutellum is short, covered with the same, fine, erect pile. The pleuron is shining black. The metapleuron, hypopleuron, and pteropleuron entirely quite bristly. Squamal fringe sparsely pilose and comparatively short. Halteres with a large knob and an elongate patch of setae at the base of the knob.

Legs: The legs are comparatively short, the tibiae, however, rather long and slender. All of the tibiae rather densely appressed, brassy setae and without bristles, although the hind pair has a ventrolateral row of some short, fine bristly hairs. Femora without bristles below, all the femora slender throughout, the hind pair with a ventrolateral row of some 10 or 12

long, coarse hairs that could not well be called bristles. The pile is setate, appressed, slightly flattened but no scales present. Claws long, slender, sharp. Pulvilli long and spatulate.

Wings: The wings are comparatively broad, narrowed at the base, broad at the apex. There are 2 submarginal cells; the first posterior cell is open maximally, the anal cell very widely open, axillary lobe and alula both narrow. The anterior crossvein lies just beyond the middle of the discal cell. The marginal cell is greatly expanded apically, broadly rounded at the apex below, meeting the costa at nearly a right angle. All of the veins are unusually stout, especially the costa, the radial trunk, and first vein. The radial trunk bears setae. There is an extra cell in both wings of my material formed by a crossvein near the end of the radial sector. Ambient vein unusually stout and complex. The wings in most species have a diffuse brownish band across the middle and sometimes the base is brownish.

Abdomen: The abdomen is remarkably broad and short and gently convex. It is much wider than the thorax, the tergites are subopaque black, a little shining in the middle and with conspicuous, though narrow opaque, cream-colored margins posteriorly. The pile consists of rather abundant, erect, moderately long, shining, fine, yellowish hair spread uniformly over the tergites and perhaps a little accentuated posteriorly and a little laterally. I find 8 tergites in the male, and the eighth being extremely short and tucked under the short seventh. Male terminalia comparatively large, thrust downward from the apex of the abdomen.

The male terminalia from dorsal aspect, epandrium removed, shows a body longer than wide, scarcely narrowed apically. Dististyli short, quite stout basally, almost triangular, convergent at apex and bearing numerous, bristly hairs. From the lateral aspect, it is longer, slender, turned upward, attenuate, pointed at the apex. The epiphallus becomes strongly swollen progressively toward the base. Epandrium, cerci, and basal apodeme all quite large.

Material available for study: I have a male of the type-species, and I also have seen the material in the British Museum (Natural History). I also have a female of *fascipennis* Bezzi sent me through the courtesy of the Cairo University, Cairo, Egypt.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no comments on adult behavior or flowers visited.

Distribution: Palaearctic: *Legnotomyia bombyliiformis* (Becker), 1906 (as *Psiatholasius*); *cineracea* Austen, 1937; *erivanensis* Paramonov, 1925; *fascipennis* Bezzi, 1925; *leyladea* Eflitoun, 1945; *palestinae* Paramonov, 1947; *persica* Paramonov, 1933; *trichorhoea* (Loew), 1855 (as *Legnotus*).

Ethiopian: *Legnotomyia striata* (Bischof), 1903 (as *Legnotus*).

Genus *Corsonomyza* Wiedemann

FIGURES 63, 64, 68, 287, 462, 497, 729, 817, 818, 819

Corsonomyza Wiedemann, Nova Dipteriorum Genera, p. 13, 1820.Type of genus: *Corsonomyza simplex* Wiedemann, 1820, as given by Bezzi, p. 3, 1924.*Lasioprosopa* Macquart, Diptères exotiques, suppl. 5, p. 82, 1855.Type of genus: *Corsonomyza nigripes* Wiedemann, 1820, as *Lasioprosopa bigotii* Macquart, 1855, by monotypy.*Pusilla* Paramonov, Proc. Roy. Ent. Soc. London, ser. B, vol. 23, p. 27, 1954b. Type of genus: *Pusilla longirostris* Paramonov, 1954, by original designation.*Denamyza*, new subgenus. Type of subgenus: *Corsonomyza ochrostoma* Hesse, 1938.

Bezzi (1924), pp. 105-106, key to 9 South African species.

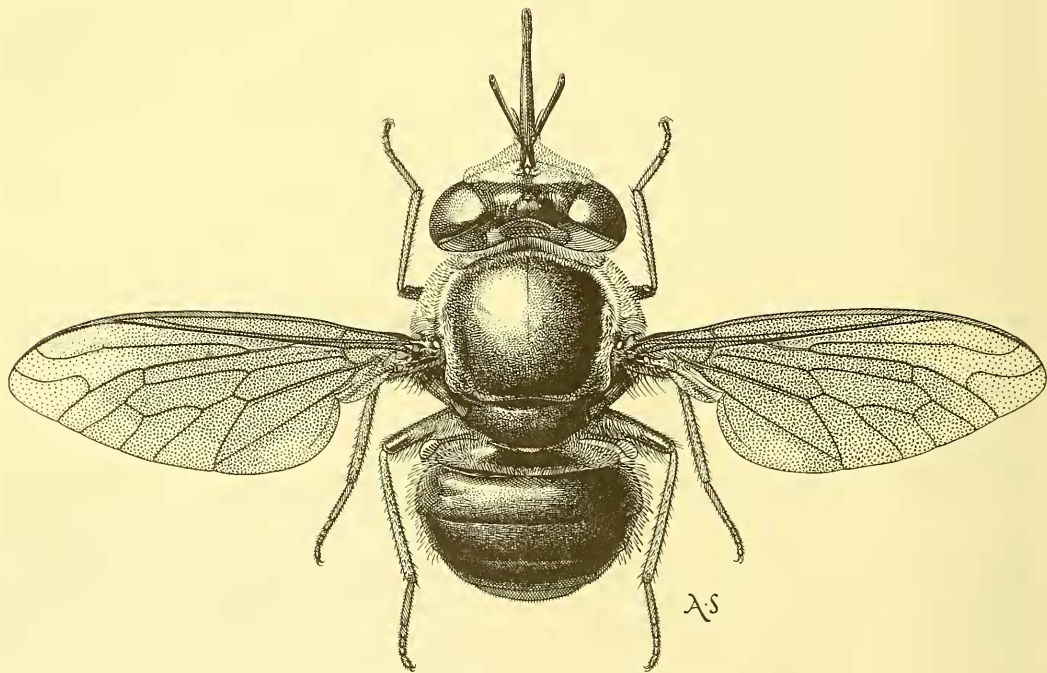
Hesse (1938), pp. 716-728, key to 13 male species and 15 female species and subspecies.

Small to medium-sized flies that are unique and peculiar in the wide or sometimes very wide head in both sexes, often wider than the thorax and the remarkably wide front in both sexes, the males being strongly dichoptic. The separation of the eyes in males is at least as wide as the wide, swollen ocellar tubercle. The front is somewhat inflated and the broad, wide face is apt to be inflated laterally. There is often a broad, wide, circular, fanlike brush of long, erect, dense pile reach-

ing in full width from the lower gena up past the face and up around to the base of antenna, and above it. This brush of pile is particularly likely to be developed in this way in males. The gena is as much expanded as the face leaving the moderately deep, rather small, oragenal cup hidden by pile. The antennae are characteristic; they are long and slender; the short first two segments have a circular band of moderately long pile all around them. The slender, elongate third segment is knob-shaped at the base; it is then quite slender beyond, but increases in width apically and becomes clavate and ends in an apical clubbed part that is grooved or hollowed out, and has a tiny apical microsegment. Male eyes sharply divided into large facets above.

Wings chiefly hyaline with basal comb and alula reduced, usually much reduced; first posterior cell open maximally; the anterior crossvein lies just beyond the apical third of discal cell; this cell is short, angularly extended below, the intercalary vein unusually long. There may be either 2 or 3 submarginal cells. The antennae lie closely adjacent.

Corsonomyza Wiedemann may be taken as the major representative of a group of characteristically South African genera not found elsewhere. The expanded genal area carrying into the face and front above is unique.

TEXT-FIGURE 22.—Habitus, *Corsonomyza simplex* Wiedemann.

It seems to be that the species *Corosomyza ochrostoma* Hesse (1938) clearly deserves subgeneric assignment, and I place it in *Denamyza*, new subgenus, derived from Greek: denaios, old, and myzo, suck.

Hesse (1938) gives the distinguishing differences thus: costal cell scarcely broadened, distinctly widened anal cell, more reduced axillary cell, distinctly raised and elevated ocellar tubercle, shorter first antennal segments, shorter labellum, distinctly longer apical spines on tibiae, several bristly hairs across last tarsal segment, much shorter than in other species, and less strongly curved claws. Found so far only in Namaqualand.

Length: 4.5 to 11 mm.; usually 6 to 7 mm. Wing a little shorter, or same length.

Head, lateral aspect: Head more or less hemispherical, the occiput short, strongly sloping inward when viewed from above to a point not greatly distant from the inner eye margin, and from this point the occiput slopes inward and forward so that it is slightly concave, but there is no large deep extensive cup as in the second division of the family. The pile of the occiput is scanty and distinctly flat-appressed, short and bristly over all of the middle of the occiput, becoming longer and shaggy at the bottom of the head. At the top of the occiput behind the vertex a row of long, conspicuous, erect, stiff hairs radiates out like a fan. The front is convex and tumid and swollen and bears conspicuously long, fine pile all across the middle portion. Beginning on the lower third it is a little reduced medially and there is a peculiar, very dense, conspicuous fringe of pile, extending obliquely forward and encircling the face and gena below, even below and around the proboscis. This odd, circular brush encloses centrally the antenna above with its long radiating circle of pile and encloses also laterally and below a dense, wide, tufted outgrowth of hair of equal length, perhaps of softer texture, and often of a different color.

The postmargin of the eye is nearly, but not quite, plane above. The eye is rounded forward and reduced in size below and with the lower third of the proboscis very much smaller and rather clearly demarcated. The proboscis is quite slender and rather long and about twice the head length with very slender, pointed, curved, microspinulate labellum. Palpus long and slender, distinctly projecting beyond the facial brush and apparently unsegmented. First antennal segment moderately long and slightly thickened and from 4 to 6 times as long as wide and always with a very conspicuous, dense, radiating circle of pile confined to the dorsal, lateral, and ventral segments of each antenna. This pile does not extend beyond the facial brush, and this segment is at most slightly thickened apically. Second segment short, robust, somewhat barrel-shaped with short setae dorsally, slightly longer setae medially and laterally. The third segment is characteristic in shape, long and slender on the basal half or sometimes more than half, either gently widened apically or rather abruptly clavate on the outer fourth or fifth and some-

times grooved on the inner margin, and sometimes with spinulose pubescence apically, or with an apical notch. The third segment is at least $1\frac{1}{2}$ times the combined length of the first two segments and sometimes longer.

Head, anterior aspect: Distinctly wider than the thorax. Approximately twice as wide as high. Eyes in the male widely separated by at least the length of the first two antennal segments. Ocellar tubercle quite large, broad, the ocellar triangle extraordinarily obtuse, the tubercle high, but gently sloping. Eye of female much more widely separated. Front convex and inflated, shining blackish, a tuft of long pile lies between the ocelli. From the anterior aspect, the facial brush, both the outer fringe and the central part are dense and plushlike, but with the facial space immediately below the antenna exposed and bare. Oral recess rather narrow and deep posteriorly. Gena extraordinarily wide.

Thorax: The thorax is quite short and broad at least as wide as long if not wider, generally opaque blackish with very dense, erect, fine plushlike pile of great length over the entire mesonotum and the whole of the short, very broad scutellum. Mesopleural pile equally dense, long, tufted and sometimes matted. Pteropleuron, hypopleuron, and metapleuron without pile.

Legs: Quite small and weak. All of the short femora bear dense fringes of long, fine, erect pile directed downward, obliquely forward, and obliquely toward the rear middle. Dorsal pile minute. Anterior tibia comparatively smooth dorsally; remaining tibia with a few, long, oblique, stiff hairs dorsally. Claws quite slender on the apical half, stout at base, sharply curved apically. Pulvilli long and wide.

Wings: Hyaline, or sometimes tinged with yellowish brown, the costal cell and the base more yellowish. Wings sometimes with an opaque, milky-white appearance. There are usually 2, sometimes 3, submarginal cells. Anterior crossvein always enters the discal cell well beyond the middle and usually near the outer third. The first posterior cell is open maximally. The anal cell is rarely open, more usually closed at the margin or with a short stalk. Alula reduced, generally narrow, even vestigial. Basal comb absent, ambient vein complete. The second vein arises abruptly at the end of the first basal cell.

Abdomen: Approximately as long as thorax, somewhat conical, narrowed and bluntly pointed apically, at the base somewhat less wide than the thorax. There are 7 tergites visible from above, the color varies from reddish brown to black, feebly shining, the pile generally extraordinarily long, fine, and quite erect over the whole abdomen, but forming a dense, long conspicuous band or fringe along the side margins. Pile varies from deep brownish yellow to white. The male terminalia are small, surrounded by long hair. Hesse (1938) states that the basimere always has an extra lobe or flap at the base and that the dististyli are clawlike, laterally compressed, and the apical part curved downward and pointed; he states that the apical lobelike part of the

aedeagus is curved upward, very uniform in the species, and without a ventral process at the base.

The male terminalia from dorsal aspect, epandrium removed, show a long, rather slender body, basally widened with extensive membranous area. The large long dististyli are convergent, rather strongly attenuate at the sharply pointed apices. From the lateral aspect the epandrium is moderately high and long, but narrows apically. Cerci small, the epiphallus stout and increasingly stout basally. Dististyli stout, sharply curved, and pointed apically. Apex turned upward. Basistylus moderately stout basally, strongly narrowing on the distal half. Basal apodeme large, except for the greater length from a dorsal aspect and its distally narrowed condition, *Corsomyza* Wiedemann shows very little fundamental difference from *Bombylius* Linné.

Material available for study: I have studied the series of *Corsomyza* Wiedemann in the British Museum (Natural History), from which my illustrations are taken, and Dr. A. J. Hesse has most kindly sent three species for dissection and study.

Immature stages: Unknown.

Ecology and behavior of adults: Hesse (1938) states that the females of *Corsomyza simplex* Wiedemann have a marked resemblance to some tabanids and are more often seen on flowers of composites.

Distribution: Ethiopian: *Corsomyza anceps* Bezzi, 1924; *ancepsoides* Hesse, 1938; *bicolor* Bezzi, 1921; *bipustulata* Bezzi, 1924; *brevicornis* Hesse, 1938; *campicola* Hesse, 1938; *capensis* Hesse, 1938; *clavicornis* Wiedemann, 1819; *depressifrons* Hesse, 1938; *dissimilis* Hesse, 1938; *eremobia* Hesse, 1938, *eremobia braunsii* Hesse, 1938; *fuscipennis* Macquart, 1840; *fusicornis* Hesse, 1938; *gonucera* Hesse, 1938; *hirtipes* Macquart, 1840; *karoana* Hesse, 1938; *longipalpis* Hesse, 1938; *longirostris* (Paramonov), 1954 (as *Pusilla*); *minuscule* Hesse, 1938; *montana* Hesse, 1938; *namana* Hesse, 1938; *nigripes* Wiedemann, 1820 [= *bigotii* Macquart, 1855], *nigripes turneri* Hesse, 1938; *nitida* Macquart, 1840; *ochrostoma* Hesse, 1938; *oneilii* Hesse, 1938; *pallidipes* Hesse, 1938; *pennipes* Wiedemann, 1820; *ruficornis* Bezzi, 1921; *simplex* Wiedemann, 1820; *tricellulata* Hesse, 1938.

As I cannot settle the exact synonymy and relationship of *Pusilla* Paramonov, I add the following comments:

Bowden (1960), in erecting the genus *Zyrmyia* Bowden, speculated that *Pusilla* Paramonov, described from Katanga, is really allied to *Corsomyza* Wiedemann, and more particularly to *Hyperusia* Bezzi. In this view, I believe he is correct. Certainly *Legnotomyia* Bezzi belongs in the Bombyliinae. For *Corsomyza* Wiedemann and its allied and related genera I have set apart the tribe Corsomyzini; *Corsomyza* Wiedemann ranges as far north as Victoria Falls, Northern Rhodesia.

These flies were described from two males taken in the Belgian Congo.

Length: 4 mm.; wing 3 mm.

I have not thus far seen this genus and I quote Dr. Paramonov's description:

Belongs to subfamily Usiinae: hind border of eyes absolutely entire; occiput very slightly prominent, not bilobate above and without a deep central cavity; occipital fringe almost absent; antennae approximate at base; prothorax and metasternum not specially developed; tibiae (femora also) only pilose, without rows of distinct spicules; all bristles on body absent. Cubital fork widely open, venation very similar to *Legnotomyia*, four posterior cells. Proboscis very long, in the type species as long as body. Palpi very thin, cylindrical, as long as mouth cavity, two-segmented, apical segment nearly bare, basal with long hairs. Two basal segments of antennae very short, rather broad and thick, first a little longer than broad, second twice as broad as long, third at least twice as long as the two basal segments together; viewed from the side, of an irregular egg-shape, at least twice as wide as second segment. Mouth cavity reaches to base of antennae, not deep, nearly as broad as sides of face; borders of cavity not high. Face very broad, equal to half of head width, frons in male also very broad, distinctly more than one-third of head width and three times as wide as ocellar triangle.

Head, thorax, scutellum and abdomen covered with very dense, long, erect hairs. Abdomen broad, oval, short, a little longer than and as broad as thorax. Hypopygium of male extremely solid and long. Two submarginal and four posterior cells. All posterior cells and anal cell widely open. Axillary cell (lobe) well developed, alula small, a little rounded, squamae long-haired. Legs without bristles.

Type of genus: *P. longirostris* sp. n.

Ground colour of body black, only basal segment of palpi, veins at base of wings, halteres, tibiae and tarsi yellowish. The long erect hairs on body yellowish-white. Hairs on occiput and face distinctly shorter than on frons. Hairs on frons intermixed with brownish hairs. Hairs on basal two segments of antennae short, third segment bare. Ocellar triangle broader than long. Viewed in profile frons not prominent, face feebly so, also the chin. Sides of frons distinctly divergent. Wings hyaline, veins in basal half yellow, in apical half darkened. Vein r-m situated distinctly beyond, but not far from middle of discal cell. Anal cell at centre only slightly broader than at base or at apex. Ambient vein complete. Alula very sparsely haired. Origin of third longitudinal vein a little nearer to common stem of radial veins than to cross-vein r-m. Legs without bristles, but at apex of tibiae and on tarsi a few black, very short spicules. Pulvilli well developed. Femora with long hairs.

Material available for study: Not seen. This genus was erected and the type deposited after our lengthy stay at the British Museum (Natural History) was concluded.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Pusilla longirostris* Paramonov, 1954.

Genus *Callynthrophora* Schiner

FIGURES 292, 480, 493

Callynthrophora Schiner, Verh. zool.-bot. Ges. Wien, vol. 17, p. 313, 1867. Type of genus: *Callynthrophora capensis* Schiner, 1868, by original designation. One species.

Hesse (1938), pp. 776-777, key to 3 species from South Africa.

A small genus of medium-sized, brownish-black or reddish-brown flies related to *Corsomyza* Wiedemann and also to *Gnumyia* Bezzi. *Callynthrophora* Schiner

has a very wide head and front and face. There is a peculiar and conspicuous inflation and tumidity on the front which extends into the face. In contrast to *Corsomyza* Wiedemann, but more like *Hyperusia* Bezzi, the antennae are attached only a short distance above the oral recess and as a result the front is even more extensive and prominent. As in *Corsomyza* Wiedemann there is a well-developed, dense, circular, facial brush: *Gnumyia* Bezzi has no distinct facial brush of pile. In *Callynthrophora* Schiner the wide, inflated, tumid front, extending lower downward, the more swollen or thickened first antennal segment, the presence of spinulose pubescence on the second antennal segment all separate it from *Corsomyza* Wiedemann. There are no long, bristly hairs on the last three hind tarsal segments such as found in *Gnumyia* Bezzi and often in *Corsomyza* Wiedemann. Usually with 3 submarginal cells, one species has only 2. The genus *Gnumyia* Bezzi differs further by the presence of a stout, fleshy labellum, very short proboscis, absence of spinules on the second antennal segment, and the presence of feathery pubescence on the hind tibia.

The 3 known species are from South Africa.

Length: 8 mm.; wing a little shorter.

Head, lateral aspect: The head is large and subglobular, with the occiput comparatively prominent but rounded in profile and also sloping strongly inward toward the foramen. Occipital pile short, scanty, bristly, but with a tuft of longer hairs near the vertex, which may also be seen from the front, rising above each eye corner. The front is light reddish brown, and greatly swollen, tumid and broadly rounded. It has numerous very long, erect hairs which continue in the same length downward upon the face but become shorter laterally on each side of the oral recess. The face extends only a short distance below the antenna but the face is as much swollen as is the front. The posterior eye margin is broadly rounded. The proboscis is slender with a slender labellum and the whole structure not longer than the head. Palpus long and slender, at least half as long as the proboscis. The antennae are attached at the middle of the head and are nearly but not quite as long as the head. The first segment is distinctly swollen and bears very long, coarse pile above and below. The second segment is small and beadlike; Hesse (1938) states that it has dense, silvery, spinulose pubescence upon its inner surface, and it may have a thornlike protuberance above. The third segment is much longer than the first two segments combined; with a knob at the base; the basal half or two-thirds is slender and filiform, the apical part clubbed or spear-shaped, of uniform thickness and nearly twice as thick as the basal part.

Head, anterior aspect: The head is very wide, wider than the thorax, and the front in both sexes much wider than in *Corsomyza* Wiedemann. At the vertex the eyes in the female are separated by 3 times the width in male. The front at the level of the antenna is remarkably wide, each half almost twice as wide as either eye. The

antennae are narrowly but distinctly separated. The ocellar tubercle is prominent although low, but the ocelli are large. The oral recess is oval, converging anteriorly below the antenna. The gena on each side of the oral recess is very wide and also wide at the bottom of the head.

Thorax: The thorax is densely covered with long, coarse, erect, yellowish pile which is more abundant anteriorly before the wing or in front of the transverse suture. The anterior suture appears to be curved from the wing in a slightly oblique, forward direction. Scutellum large and thick and convex, with a deep basal crease; its surface bears numerous bristly hairs with similar hair distributed over the margin. The upper half of the mesopleuron is irregularly covered with very dense tufts of long, coarse, brownish-yellow pile. The propleuron and the middle of the sternopleuron bears a little, scanty, scattered tuft of similar pile. Remainder of pleuron bare. Squama short with a dense, thick fringe of fine hairs. There appears to be no anterior collar of pile upon the mesonotum, and bristles are absent on the thorax.

Legs: All the femora are slightly thickened, the tibiae likewise stout. Anterior femur with some long, coarse pile distributed along the ventral surface. Middle femur with a rather dense anterior and posterior fringe of long, coarse pile extending close to the ventral margin. The hind femur has scattered, bristly hair laterally and some longer, similar bristly hair near the apex which is distributed ventrolaterally. The anterior tibia has 3 or 4 dorsal bristles and 5 or 6 minute, posteroventral bristles; middle tibia with four anterior bristles, 6 posterodorsal bristles, and only 2 or 3 minute, posteroventral bristles. The hind tibia has distinct, long bristles laterally and very short medial bristles; it has 12 or 15 dorsomedial bristles some of which are scarcely differentiated from the setae pile, and it has a like number of ventromedial bristles; there are present 12 dorsolateral and 7 ventrolateral bristles. The tarsi end in slender, sharp, gently curved claws and well-developed pulvilli.

Wings: Hyaline, comparatively short and relatively broad apically. There are 3 submarginal cells within the type-species and also in *hastaticornis* Hesse; the species *marginifrons* Bezzi has only 2. The first posterior cell is opened maximally or even widened on wing margin; anal cell wide, acute, closed in the margin or with a short stalk. There is no basal comb. Ambient vein complete and alula narrow.

Abdomen: The abdomen is short oval, or obconical, not quite as wide as the thorax and covered densely along the sides with long, coarse, pale pile which extends along the extreme lateral margin as a brush covering the sternites. The pile upon the dorsum of the abdomen is considerably less extensive and is a little shorter. The abdomen is opaque, dark, brownish or blackish in color and brownish black pollinose.

Hesse (1938) points out that the hypopygium is like that of *Corsomyza*, the basimere shows a posterior lobe,

the beak on the dististyle is acute but much less laterally compressed, the band of hair along the upper dorsal part less dense; the aedeagus more acute apically, from the side less broad and without lateral process.

Material available for study: Representatives in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Callynthrophora capensis* Schiner, 1868; *hastaticornis* Hesse, 1938; *marginifrons* Bezzi, 1921, and also *magnifrons*, erratum on plate explanation, p. 180.

Genus *Gnumyia* Bezzi

FIGURES 289, 483, 506

Gnumyia Bezzi, Ann. South African Mus., vol. 18, p. 82, 1921a.

Type of genus: *Gnumyia brevisrostris* Bezzi, 1921, by original designation.

Hesse (1938), pp. 781-782, key to 2 South African species.

Small to medium-size flies that are very remarkable from having a peculiar ensemble of characters. There is a remarkable inflation of the face, sides of face and genae, the more striking since the antennae are attached high up on the head, a great deal nearer the ocelli than to the oragenal cup. The whole head is much widened, wider than the thorax, and most of this unusual head width reflected in the exceptional width of face and front. Male eyes strongly separated. The greater part of the inflation of the face lies below the antennae; moreover, it has the antennae rather widely separated at base, at least as much as width across posterior ocelli and the second segment lacks spinulate pubescence, the third segment is scarcely or not at all clavate at the apex; the proboscis is very short, stout, with fleshy labellum. In its nearest relative, *Callynthrophora* Schiner, the reverse is true; there the most conspicuous and exceptional part of the swelling of the equally wide head lies chiefly on the front above the antennae, which are attached side by side. The antennae have marked spinulose pubescence on the second segment and a dilated apex on the third segment; its longer, more slender proboscis and labellum and its legs lack the dense, feathery pubescence on the hind tibiae, which is found upon *Gnumyia* Bezzi. Known species of *Gnumyia* have 3 marginal cells. The dististyli of the hypopygium are less clawlike than in *Callynthrophora* Schiner.

These flies are part of a very remarkable and characteristically South African section of the subfamily Bombyliinae, including, besides those mentioned above, *Corsomyza* Wiedemann (with the most species), *Megapalpus* Macquart, and *Hyperusia* Bezzi.

Length: 5.5 mm. to 8 mm.; wing a little shorter.

Head, lateral aspect: The head is subglobular in shape due largely to the remarkably swollen front, face, and gena; the occipital part is not extensive. The oragenal cup is not only small but extraordinarily low, and because of this the face is extensive and high; it is at

least as high as the length of the antenna. The pile of the face is loose, yet abundant, and is coarse, blackish and comparatively long, the shining, yellowish-brown ground color not obscured. There is no dense brush of pile formed as in other *Corsomyzini*. Occiput short and poorly developed with rather dense, short, fine, submarginal pile. The eye much narrower than high, appears smaller perhaps as a result of the great development of face and gena; its posterior margin is entire. The thickened proboscis is quite short, extending barely beyond the face, except when thrust downward; labellum short, fleshy, tumid. Hesse (1938) says of the labellum that it is broad and more like a muscid, bears conspicuous, scattered spinules. The palpi in *Gnumyia* Bezzi are shorter than the proboscis. The front is convex and bears pile similar to but shorter and less dense than that of the face. The antennae are attached at the upper two-thirds of the head; they are relatively slender, of uniform thickness, and moderately long, but at most only two-thirds as long as the head. The first segment is a little more than twice as long as wide, the second segment is beadlike with upper apex extended in a styliform process. The first segments are quite widely separated, more so than in other *Corsomyzini*. The third segment, narrowed at the apex, bears a short, conical microsegment.

Head, anterior aspect: The head is quite wide in consequence of the extensive face and very wide genae, and it is wider than the thorax. The eyes are narrowed anteriorly and quite concave on the medial border. Eyes widely separated in the male, in fact Bezzi, who described the genus from a single individual, thought that he had a female, when in reality he had a male before him. The vertex is elevated and swollen and the ocelli large. Orogenal opening small, narrow, and slitlike and situated at the bottom of the head. The extensive face is separated from the wide gena by a furrow, becoming deeper below. The occiput is broadly and shallowly concave dorsomedially, and there is no medial dorsal fissure.

Thorax: The thorax is rather flattened, with fine, long, erect, dark pile along the sides; bristles absent but margin of scutellum with a few long, bristly hairs. The scutellum is quite convex, large and exceptionally thick. Metapleuron entirely bare, and tuft below the halteres likewise absent; mesopleuron very densely long, coarse, blackish pilose. Squamae with a long, not very dense fringe; no distinct plumula present.

Legs: The femora are slender, the tibiae likewise. Hind femur laterally, medially, and ventrally with rather long, coarse pile, dense below; bristles absent. Middle and posterior tibiae with anterodorsal and posterodorsal rows of fine, long, bristly hairs, but only a posterodorsal row on anterior tibia. Hesse describes some of these elements as "stoutish spinules" on anterior and other tibiae. The tarsi are moderately slender; last segments with more than 3 hairs apically and above. Claws small, sharp, a little curved, the pulvilli well developed with a short, triangular medial lappet.

Wings: The wings are hyaline or with brownish tint, almost identical with *Callynthrophora* Schiner and likewise with 3 submarginal cells; however, the alula, while narrow, is a little wider. The first posterior cell is widely open, in fact wider at the end than at base or middle; the second and third posterior cells widely open. Discal cell relatively short, widened and angulate below; the anterior crossvein lies barely beyond its middle. Upper end of third posterior cell strangely arched and convex. Anal cell closed in the margin or with very short petiole. There is no basal comb; the costa is densely short pilose at base. Ambient vein complete.

Abdomen: The abdomen is quite broad at the base, as wide or a little wider than the thorax and rather strongly narrowed to the end of the fourth segment. The specimen before me seems to have the abdomen a little distorted apically on the left side, but there seems to be a degree of normal, lateral compression of the terminal abdomen. The fifth, sixth, and seventh tergites are nearly parallel-sided. There are 7 tergites with the seventh being three-fourths as long as the sixth. Pile of the abdomen very fine, moderately long, somewhat bristly in character and quite scanty, except along the lateral margins, where it is a little more abundant and, except on the lateral third of the first and second tergites, where it is rather dense. Last sternite of male notched apically.

Hesse found the dististyli rather triangular seen from above, the outer side much produced, the beak distinct and slender; the points not laterally compressed but distinctly compressed dorsoventrally; the basal part on both known species roughened and having fine hairs. Aedeagus like other *Corsomyzini* and without a ventral process; lateral and basal struts small.

Material available for study: Of this rare genus I have for study only a male of *Gnumyia brevirostris* Bezzi in the British Museum (Natural History) from which my figures are taken. Two species known; the material studied by Malloch may represent a third species. Only males so far known.

Immature stages: Unknown.

Ecology and behavior of adults: Adult habits not recorded.

Distribution: Ethiopian: *Gnumyia brevirostris* Bezzi, 1921; *fuscipennis* Hesse, 1938.

Genus *Hyperusia* Bezzi

FIGURES 62, 295, 492, 500

Hyperusia Bezzi, Ann. South African Mus., vol. 18, p. 84, 1921a.

This is the first mention of this genus. Description and type of genus in: Bombyliidae of the Ethiopian Region, p. 107, 1924. Type of genus: *Hyperusia luteifacies* Bezzi, 1924, by original designation.

Hesse (1938), pp. 765-767, key to 6 South African species.

Small, blackish flies, the face sometimes partly and the antenna also in part orange or reddish in some

species. It is separated from *Megapalpus* Macquart by the nonprominent buccal rim of the oragenal cavity; this cavity rim does not conspicuously and clearly protrude forward as it does in the latter genus. The antennae are less widely separated, the first segment distinctly shorter, and the proboscis is shorter and noticeably thicker basally. The male eyes are more narrowly separated, the distance between being of the approximate order of *Corsomyza* Wiedemann, to which *Hyperusia* Bezzi is also related.

This genus does have loosely scattered, numerous, long, coarse hairs on all of the front except a narrow medial portion near the antenna and upon the whole sides of the face and the very wide cheeks. Nevertheless, it is loose and scattered, never hiding the surface of the head. Wings hyaline with very pale veins, 2 submarginal cells, the 4 posterior cells all widely open and with the anterior crossvein entering near the outer fourth of the discal cell. These rather small, dark colored flies are covered with rather abundant, long, fine, erect pile but in addition have on the abdomen some sparse, flat-appressed, shining, slightly flattened hairs. The abdomen is broad at the base, slightly narrowed, more so on the last two segments and about 1½ times as long as wide. Vertex separated from the front by a distinct, rather deep, sharp, transverse crease or fovea.

The body of these flies is rather bare and the pale pile sparse, stiff, and almost spikelike upon the face and front and antennae. As Bezzi (1924) points out, there is no facial brush and the whole face and front are relatively bare; the legs are rather stout and short, without bristles.

The femoral hair, while fine, is more abundant than in *Megapalpus* Macquart even in the female. There are 3 long, apical hairs across the apical margin of the last tarsal segment as in *Corsomyza* Wiedemann. The last male sternite is notched at the middle as in both these related genera. The male terminalia are much like *Corsomyza* Wiedemann; unlike that genus the head in front is not conspicuously broadened, the sides of the face, and the gena not conspicuously tumid and prominent. The antennae are inserted much lower down upon the face.

Other characteristics consist of antennae inserted very close to upper oragenal rim; oragenal rim and cup not protruding as it does in *Megapalpus* Macquart, and the proboscis much shorter than in *Megapalpus* Macquart. While the body of the species is blackish the legs and the antenna tend to be in part pale yellow or red, and the contrast in color is heightened by the often stiff, sometimes stubb-tipped and frequently opaque whitish or yellowish pile. A small metapleural tuft is usually present; last tarsal segments with at least 1 long hair.

Hyperusia Bezzi is a small genus of 6 species from South Africa. Hesse (1938) notes that the type-species may be a true *Corsomyza* Wiedemann of the *simplex* Wiedemann series, and notes further that the other species are abundantly distinct.

Length: 3 to 7 mm., of wing 3 to 5.5 mm.

Head, lateral aspect: The head is comparatively short, somewhat rounded behind, more so in front. The occiput is poorly developed posteriorly, although there is a small, deep, central, cuplike recess leaving the intervening area quite wide and extensive when viewed from the rear and covered with dense, short, erect pile growing much shorter toward the eye margin. The face is short in profile but quite wide, bisected by the oragenal cup which reaches to the antenna but is itself short and inconspicuous. Along each outer margin of the oragenal cup between the face and cheeks is a more or less large, sunken area which is apparently the sole remnant of the tentorial pits for there are no fissures above or below. Posterior eye margin almost entire with the merest suggestion of a middle depression.

The face and front are continuous; both bear moderately dense, long erect, coarse, stiff, pale pile. This pile is somewhat longer on the swollen front but is absent medially on the anterior half of the front. The whole of the vertex is occupied by a rather prominent, exceptionally broad, ocellar tubercle or ridge set off anteriorly by a transverse crease or fovea. The ocelli are well developed, though small; the posterior pair is unusually widely separated. The long, loose stiff pile of the face is continued upon the cheeks and the whole of the lateral genofacial depression. The palpus is elongate, slender, and laterally bears a number of conspicuous, long hairs. The second segment is a little widened. Proboscis slender, attenuate at the apex and extending a short distance beyond the antenna. The antennae are attached at the middle of the head; the first segment is twice as long as the beadlike second segment; third segment elongate, widest at the outer third, then a little narrowed to the blunt apex; it is without terminal style.

Head, anterior aspect: The head is much wider than thorax and considerably wider than high, much of which is doubtless occasioned by the remarkably wide face found in this group genera. The oral opening is about one-third the total face width and is $1\frac{1}{2}$ times as wide as long, strongly narrowed on the upper portion extending to the antennae. The antennae are narrowly separated by perhaps the basal width of the first segment.

Thorax: The thorax is about as long as wide excluding the large scutellum. It is more or less shining, usually blackish and loosely covered with long, fine, erect pile, including the humerus and there is similar long tufted pile on all, except the lower portion of the mesopleuron. There are a few long hairs posteriorly on the pteropleuron, the metapleuron appears to be bare. Bristles absent.

Legs: The femora are slightly thickened through the middle. The anterior femur bears minute, appressed setae anteriorly but coarse, long, rather sparse hairs dorsally and posteriorly. The middle femur bears similar long hairs in front and behind and below but short hairs dorsally. Hind femur with short, appressed hairs

dorsally and rather fewer, fine, long hairs ventrolaterally. All of the tibiae with fine, scattered, subappressed pile. The dorsal surface of the hind tibia has a longer, more conspicuous fringe; last tarsal segment with 3 long hairs, spicules absent. Claws fine, pulvilli well developed; the arolium forms a minute stub.

Wings: The wings are hyaline with extremely pale, whitish-yellow veins, the surface minutely villose; there are 2 submarginal cells; the 4 posterior cells are all widely open, the anal cell narrowly open, the alula well developed, the ambient vein complete. The second vein arises at the base of the discal cell and the anterior crossvein enters the discal cell near the outer fourth. The wing is rather short and broad, especially basally. The costa is a little expanded triangularly at the base and has a rounded, cup-shaped, somewhat beaklike lobe at the base.

Abdomen: The abdomen is a little longer than the thorax, wide at the base, slightly narrowed and more strongly narrowed at the apex. The tergites bear scattered, quite long, delicate and fine, erect hairs a little more abundant toward the sides of the first three tergites and forming, however, a conspicuous, loose, marginal fringe along the lateral margins of all of the tergites. On the surface of the tergites, more dense and conspicuous on the posterior half of the abdomen, there are fine, flat-appressed, somewhat curled, glittering, smallish hairs.

Hesse (1938) describes the male terminalia:

... much like *Corsomyza* Wiedemann; basal part of basimeres likewise with a rounded lobe-like part; distimeres (beaked apical segments similar) much compressed laterally, claw-like, the acute apex curved downward. Aedeagus similar, also, without a ventral process ending basally above the middle part in a lobe-like process. Basal struts more or less racket shaped, the dorsal margin deeply and angularly incised toward the apex.

Material studied: The type-species *luteifacies* Bezzi, in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Hyperusia luteifacies* Bezzi, 1924; *minor* Bezzi, 1921; *musoides* Hesse, 1938; *nivea* Hesse, 1936; *soror* Bezzi, 1921; *transvaalensis* Hesse, 1938.

Genus *Megapalpus* Macquart

FIGURES 67, 288, 485, 505, 742

Megapalpus Macquart, Suite à Buffon, vol. 1, p. 394, 1834. Type of genus: *Phthiria capensis* Wiedemann, 1828, by monotypy. *Dasypalpus* Macquart, Diptères exotiques, vol. 2, pt. 1, p. 112, 1840. Type of genus: *Phthiria capensis* Wiedemann, 1828, by monotypy, female, as *Dasypalpus capensis*.

Hesse (1938), p. 761, key to 2 South African species.

Small, shining blackish flies, quite bare in appearance with fine, short, silky, depressed, scanty pile on mesonotum and abdomen of the females and the males with scanty erect hairs, and few or no depressed ele-

ments. The abdomen is short, apically rounded, and rather convex. There is one weak bristle on the notopleuron and an odd radiating tuft of long, coarse pile on the upper border of the mesopleuron. Face wide but much less wide than in *Callynthrophora* Schiner and *Gnumyia* Bezzi, and not tumidly swollen as in those genera. Moreover, the face is well developed above the moderately high oragenal cup, in contrast to *Hyperusia* Bezzi where the oragenal cup reaches quite to the antenna. The face in *Megapalpus* lacks the curious, striking circular brush of long, dense hair which is so characteristic of *Corsomyza* Wiedemann. Wings small, broad, and hyaline with heavy dark veins and the posterior cells short and wide and widely open; costal comb absent; 2 submarginal cells present; the anterior cross-vein enters the discal cell beyond the middle. Hind femur with microsetae below but all tibiae with spicules. Finally the interocular space on vertex is quite wide in both sexes. More closely related to *Hyperusia* Bezzi but sharply differing in the character of the face and oragenal cup and to some extent in the antennae. The third segment of *Megapalpus* Macquart is regularly and gradually dilated to the apex ending in a lipped cup and concealed spine and in *Hyperusia* Bezzi. It is distinctly obliquely truncate and tapered beginning at the outer fourth. In females of *Hyperusia* Bezzi there is considerably more pile above on the body than in females of *Megapalpus* Macquart.

This small genus is confined to South Africa.

Length: 3.5 to 6 mm.

Head, lateral aspect: The head from the lateral view is, apart from the extensive oragenal cup, more or less short oval. The very large eye is not much higher than wide and posteriorly curves strongly inward so that the short occiput is further reduced by this inward retreat of the eye. The occiput is, then shallow and only slightly depressed where the head joins the thorax. The pile is quite short, scanty, fine, and curved outward toward the eye margin throughout. The face is extensive below the antennae but bare, polished and shining, and appears to be divided by a shallow, transverse furrow on the lower two-thirds; beyond this furrow the face forms an added component to the very deep, large, more or less circular, sharp-walled extensive and protrusive oragenal cup. The pile along the wide flat genae is abundant though loose, long, erect, stiff, pale and extends from the bottom of the eye up to the base of the antennae with similar pile continued, though shorter, on the sides of the front.

Posterior margin of the eye entire but not plane. The proboscis is unusually long and unusually slender with minute, long, slender labellum; it is about 3 times as long as the head. The palpus is unusually long and quite slender. Its length from the bottom of the oral opening as long as the antennae. The front is very wide, as wide or a little wider than either eye, somewhat flattened across the middle and bearing very fine, erect, blackish hairs on the dorsal half mixed in with which are some shorter, flattened, curled, subappressed hairs,

and laterally on the lower half loosely scattered, long pale hairs like those on the genae. In addition on the lower part of the front at the eye margin there is in females a curious tuft of very dense, matted, subappressed, long, silvery or yellowish scalelike hairs. Middle of front coarsely appressed, scaliform micropubescence in the middle and more densely between the antennae. Remainder of front and the vertex likewise shining and bare. The long black bristles of the front extend onto the vertex. The antennae are attached near the upper third of the head. Antenna slender and about as long as the head or perhaps a little shorter.

The first segment is rather slender, a little widened apically, at least 3 times as long as the apical width and bears several long, bristly hairs and 1 or 2 bristles dorsally along the middle. It also bears several still longer hairs laterally or ventrolaterally, but there is no conspicuous pile or bristles extending downward from below. The second segment is short and beadlike, widened apically. The third segment has a peculiar and characteristic shape; just beyond the base it begins to be narrowed, and on the outer half it is gradually and slightly widened and swollen until it is clublike. However, from the lateral aspect it is not narrowed but only gradually widened. At the apex it bears a short, dorsal, subapical spur rather than a microsegment, which appears to have a small recess within it. The apex of this segment is notched, and the ventral portion is blunt and extends very slightly beyond the dorsal lobe or spur.

Head, anterior aspect: The broad head is much wider than the thorax. The eyes are widely separated in the male, almost as widely separated as in the female. In fact the inner ocular distance in the male across the plane of the anterior ocellus is as great or greater than the width of either eye. The antennae are widely separated at the base by more than twice the thickness of the first antennal segment. The ocellar tubercle is low and small, the ocelli are likewise small. The oral opening is quite large, deep, with the wall thin, knifelike, and protruding a considerable distance down below the eye margin. The interior recess is flattened or very slightly concave and smooth, without conspicuous ridges and without pile. The gena is moderately well developed, about as wide as the thickness of the third antennal segment and shelving inward to the tentorial fissure only along its medial edge.

Thorax: The thorax is quite shallowly convex, except along the anterior margin, which is very abruptly raised above the short pronotum. The whole thorax is shining black with a little faint pollen on the anterior declivity. The mesonotum bears a few, fine, quite loosely scattered, erect black hairs and in addition some equally sparse, short, curled, appressed, brassy hairs. Scutellum similar, the black bristly hairs longer, especially along the margin and also few in numbers. The sides of the scutellum and the prescutellar declivity are gray pollinose. There are no notopleural bristles. The pleuron bears a very conspicuous tuft of dense, long,

coarse, slightly flattened pile. About half of this pile is directed anteriorly and dorsally, the other half posteriorly and downward. The upper sternopleuron has a tuft of loosely scattered, fine, short, erect hairs. Pteropleuron, metapleuron, and hypopleuron entirely without pile, except that the hypopleuron has 2 or 3 hairs beneath the spiracle. The propleuron is almost entirely bare.

Legs: The legs are unusually short. The femora are all short and relatively stout with coarse, fine, suberect setae. Hind femur with a few longer stiff hairs below which are scarcely bristly. Anterior tibia without isolated spicules and with only fine setae, a few of which are suberect. Hind tibia with 5 or 6 slender bristly hairs along the anterolateral margin. Tarsi quite short, pulvilli large, long and wide. Claws gently curved from the base.

Wings: The wings are relatively short and moderately wide with the veins thick. There are 2 posterior cells but the second posterior cell is rather short, the anterior branch of the third vein arises rectangularly, and proceeds forward for some distance, then bends strongly, and the remainder of this vein is straight. Marginal cells slightly widened apically, the second vein only gently curved on the outer part. Anterior crossvein enters the wide discal cell at or beyond the outer third. The anterior intercalary vein is long. The first posterior cell is wider on the wing margin than elsewhere. The anal cell is remarkably widely open, the axillary lobe narrow. Alula linear and almost absent. Basal comb weak or absent. The basal spur or hook small. Ambient vein complete.

Abdomen: The abdomen is short and tapered, very slightly convex over the middle, more so laterally. It is shining black with pile quite similar to that of the mesonotum and scutellum. The erect, stiff, or slightly bristly hairs are few in numbers even along the curled side margin and on the second to the fourth tergites, as far as the lateral margin is concerned, they are restricted to the posterior corners, leaving tufts of short, loose, erect, pale colored pile along the remainder of the lateral margin and this pile does not extend inward along the middles of the tergites, except on the first segment. Middles of remaining tergites with a few brassy, slightly flattened, curled, and appressed hairs. I find 7 tergites in the male, the last nearly as long as the preceding. The terminalia are large, tucked into the right beneath the last several segments.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium of males like that of *Corsomyza*, the basal parts with a posterior lobe; the beaked apical joints laterally compressed, acutely pointed apically and with a crest of spine-like, bristly hairs along their dorsal (upper) parts; aedeagus much like that of *Corsomyza*-species, without any ventral aedeagal process.

Material available for study: A male of the type-species given to me through the courtesy of Mr. Harold Oldroyd of the British Museum (Natural History) and

another through the kindness of Dr. A. J. Hesse. The series of this genus was also inspected at the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Megapalpus capensis* (Wiedemann), 1828 (as *Phthiria*); *fulviceps* Bezzi, 1921; *nitidus*, Macquart, 1840.

Genus *Zyxmyia* Bowden

FIGURES 294, 546, 770

Zyxmyia Bowden, Journ. Ent. Soc. South Africa, Pretoria, IV, vol. 23, p. 213, 1960h. Type of genus: *Zyxmyia megachile* Bowden, 1960, by original designation.

Small, black or blackish-brown flies, very similar in general to *Megapalpus* Macquart. The oragenal cup is extensive and prominent, the proboscis long and slender. The face and vertex are quite wide even in males, presently the only captured sex. The antennae are separated by the length of the first two segments. Bowden notes that the short, globular, basal antennal segment is placed close to the upper part of the oragenal cup, and the denser pubescence and absence of stout, alar bristle ally this form to *Hyperusia* Bezzi. Like *Hyperusia* Bezzi and some species of *Corsomyza* Wiedemann it has an excavated third antennal segment; with *Corsomyza* Wiedemann it has a rapidly divergent eye margin; its front, Bowden states, is at the level of the antenna, at least half again as wide as at the vertex. It differs from all other genera in the structure of the legs, especially the incrassate femora, the thorns on the tibiae and the unique, divided, first abdominal tergite. Bowden felt that it stood closest to *Megapalpus* Macquart, and distinguished from it by the position of the antenna, divergent eye margins, more dense pubescence especially upon the pleuron, and by the absence of a bristle at the base of the wing.

This fly is known only from males from Tanganyika at elevation of 4,850 feet.

Length: 6.8 to 8.3 mm.; of wing 6.7 to 8.0 mm.

I have not seen these flies and I quote the author's description:

Allied to *Corsomyza* Wiedemann, *Hyperusia* Bezzi and particularly to *Megapalpus* Macquart. Body with fine erect pubescence on thorax and abdomen and with adpressed hairs, at least in male, denser on abdomen; pleurae with comparatively dense hair on mesopleurae and with short fine hair on pteropleurae and sternopleurae; metapleurae bare, no metapleural tuft. Head with interocular space very broad in male, frons ridge-like either side of ocellar tubercle, very broad, eye margins divergent, frons notably wrinkled especially near antennae; facial area more or less parallel-sided with sparse, fairly long hair but no facial brush, genae comparatively broad, buccal rim prominently produced; antennae inserted moderately far apart (about $\frac{3}{4}$ distance between posterior ocelli of genotype) just above buccal rim, first two segments short, subequal, more or less globular, second without or with only very small dorsal process, third segment long relative to first two, broad and strap-like, excavate on inner surface, apex appearing some-

what bifid by reason of a subapical, dorsal pit which contains a minute but stout style; eyes comparatively large, facets equal, at least in *Zyomyia megachile*; proboscis very long and stout, palps apparently with one segment, long and slender, club-shaped at apices.

Thorax with a small hair tuft on mesopleurae, without any macrochaetae; scutellum clothed as thorax, without any long, bristly hairs. Abdomen with first tergite split medially, second prominently ridged, other tergites with median transverse depression; abdomen at least as broad at tergite two as thorax, tergites VII and VIII reflexed beneath abdomen, thus only six tergites visible from above; last sternite with small, median, apical notch. Legs with femore markedly incrassate, tibiae and tarsi also stout; without spines or spicules except for some antero-ventrally on hind tibiae; with only very short pubescence; fore and mid tibiae with a postero-dorsal row of very short, stout and heavily sclerotised thorns and similar, but somewhat more slender thorns ventrally on basal tarsal segments of mid and hind legs; last tarsal segments without apical long hairs; claws very stout, widely divergent, strongly bent, pulvilli large, empodium strongly developed, as long as pulvilli.

Wings about three times as long as broad, long in relation to body length; with two submarginal cells; discal cell notably broadened in middle, anal cell closed before wing margin and shortly stalked; alula reduced but lobe-like; costa slightly broadened at the base but basal comb absent. Hypopygium of *Corsomyza* type: basal parts rounded, shell-like, with a posterior lobe, beaked apical joints compressed, pointed, without bristly hairs; aedeagus without ventral process, lateral rami asymmetric.

Material available for study: Not seen. Types in the British Museum (Natural History).

Immature stages: Bowden (1960) speculates that it may parasitize species of *Megachile* Latreille.

Ecology and behavior of adults:

The area in which it was captured, northeast of Lolkissale in Northern Tanganyika, contains some of the desert and semi-desert vegetation type of Gillman (1949), the flora of which consists in part of succulents; it would thus appear that *Z. megachile* favors a habitat very similar to the Karoo-type habitat frequented by its southern relatives. It bears a great resemblance to the smaller, brownish species of *Megachile*, such as *gratiosa* Grst., *discolor* Sm., and *semivenusta* Ckll., upon which it may well be parasitic, and to which the trivial name makes reference as well as to the prominently produced buccal rim.

Distribution: Ethiopian: *Zyomyia megachile* Bowden, 1960.

Genus *Mariobezzia* Becker

FIGURES 291, 488, 496

Mariobezzia Becker, Ann. Mus. Zool. Acad. Imp. Sci., St. Petersburg, vol. 17, p. 470, 1913a. Type of genus: *Mariobezzia zarudnyi* Becker, 1913, second of two species, by designation of Bezzi, 1924.

Eflatoun (1945), pp. 60-61, key to 2 species.

Small to medium-size flies readily distinguished by the 3 submarginal cells, the very bare aspect with considerable pale coloration, and the unique face. The middle third of the face, which is very extensive dorso-ventrally, is extended forward as a prominent, protrusive, nose-shaped extension, separated from the excep-

tionally wide frontogenal region by a deep crease. On this account Eflatoun (1945) likens the face to that of a conopid. The oral recess in consequence is small and is situated quite low upon the head; from it the short, proboscis is extended; this varies in length from less than the length of the head to about equal to the head length. The male eyes are widely separated and the face and front quite wide in females. The front is shining and waxy white to honey yellow or even light brownish. The face is apt to be blackish in the middle at least. The thorax is mostly black in males; sometimes with pale vittae in females of *catherinae* Eflatoun. The medial keel of the face is separated from the genae, which Eflatoun curiously describes as narrow, by deep fissures in which probably lie the tentorial pits or seam. Antenna elongate; third segment more than twice the length of the basal segments, of nearly uniform width, except that it bears a short, dorsal, preapical style or spine. Second segment at apex in females, sometimes in males, with a short, dorsal spinelike process.

Both *Mariobezzia* Becker and *Corsomyza* Wiedemann have expanded gena but there is no conspicuous facial brush in *Mariobezzia* Becker, its face being almost nude, shining, bare, and polished. The real relationship appears to be with the *Corsomyzini*; though it is unique it is no more so than other genera within the Bombyliinae, and I can see no reason for creating a separate subfamily for it; I therefore reduce its status to that of a tribe, within that subfamily. Indeed, since both *Mariobezzia* Becker and *Corsomyza* Wiedemann and its allies share in most species and sexes a distinct, thorn-like projection anteriorly from the top of the second antennal segment, it would appear that they are closely related. Probably both should be assigned to a single tribe, the name of which would have to be *Mariobezziini*. Eflatoun (1945) has given a very complete description of both *lichtwardti* Becker and *catherinae* Eflatoun from large series. Among the female variants in his mated series were individuals answering to the description of *zarudnyi* Becker, *pellucida* Paramonov, and *griseohirta* Nurse, all of which he places in synonymy. Although Eflatoun placed *zarudnyi* Becker, the type-species, as a synonym of *lichtwardti* Becker, it appears that the reverse would be true. He listed *lichtwardti* as type-species.

Mariobezzia Becker is a Palaearctic genus of a few, highly variable species, according to Eflatoun, with numerous synonyms. Eflatoun (1945) notes that the type-species has been taken sparsely in Persia, Asia Minor, Egypt, the Sudan, and South India but is common only in Egypt.

Length: 2.3 to 10.8 m., very variable; wings expanded 4.4 to 12.8 mm., with marked differences in color and size in sexes.

Head, lateral aspect: Face rather strongly produced as an exceptionally wide, high, arched, convex ridge, which occupies not quite half the total width between the eyes and which develops a short distance below the antenna and is demarcated by a deep, vertical crease

extending all the way to the lower part of the face. This lateral portion, which may be regarded as the expanded gena, ranges from waxy white to honey yellow and it is shining and gently convex. The middle portion may be yellowish brown and shining, with a diffuse, medial, brown stripe. The sides of the face, as well as the middle, have dense, rather long, fine pale pile that is continued onto the anterior half of the front. The oral opening is small, nearly horizontal, $2\frac{1}{2}$ times as long as wide, the opening extends back to the posterior margin of the occiput. The proboscis is short but with the terminal labella large and convex ventrally, plane dorsally, and apically rounded, with lateral and ventral bristly hairs. The palpi are very small, short, cylindrical, composed of one segment. The eye is strongly narrowed below, and posteriorly it is narrowly and gently recessive at a point near the upper third. The occiput is short everywhere and extremely short above the dorsal third, with a broad deep vertical concavity extending from the bottom to the vertex, the latter without medial fissure, and with a crease extending to the corner of each eye.

Head, anterior aspect: The front is rather abruptly narrowed, shining white, or with a diffuse, blackish spot, a little inflated. The ocellar tubercle is rather strongly swollen above the eye, the ocelli reaching nearly to the eye margin and are situated in an obtuse triangle with long erect dorsal pile between the ocelli which is rather abundant. Antennae attached at the upper fifth of the head, rather long and slender, the first two segments are quite short, of equal length and bearing fine terminal bristly hairs. Third segment slender but of nearly uniform width to the middle, then gently tapered to the apex which is sharply pointed with a short, pointed microsegment. The whole dorsal surface is plane. Dorsally at the apex of the second antennal segment, females always and males almost always have a distinct, forward-thrust spine or process.

Thorax: Densely, long, fine, pale pilose, the shining black ground color not obscured. Females of *catherinae* Efllatoun have a whitish to citron yellow thorax with 3 black vittae. Bristles are absent. The scutellum is large, exceptionally thick and convex especially along the margin and there is a deep basal crease and the whole surface and margin have numerous, fine, long, erect hairs. The mesonotal pile is fine and erect, white in some species, darker in others. The mesopleuron and pteropleuron bear dense, long coarse, pale pile; remainder of pleuron without pile; squamae with a fine fringe of delicate hair.

Legs: The legs are rather short, the femur moderately stout without being swollen, the tibiae slender, the hind femur with a ventral fringe of long coarse hair, its tibia with a similar fringe especially laterally. Middle tibia with anterior and posterior dorsal fringe of 10 or more slender pale bristly hairs; these hairs are much shorter, finer, and present only posteriorly on the anterior tibia. Claws very slender, especially at the base, sharp, the

pulvilli well developed and with a short, triangular, medial lappet.

Wings: The wings are hyaline, broad, especially so on the basal half. The anal cell is closed and bears a short stalk. The branches from second and third veins which meet may join into a single vertical vein sectioning the first submarginal cell so that there are 3, or the posterior branch of the second vein may be emitted quite obliquely. Axillary lobe quite broad, the alula of medium width. The venation is very similar to *Corsomyza* Wiedemann.

Abdomen: Shining blackish with shining yellow posterior margins to the first three or four tergites of males. The abdomen in females is rather strongly cylindrical, quite convex and gently tapered to the end of the fourth tergite, a little more strongly beyond. The color in females is highly variable but often largely whitish yellow or yellow with black, subbasal bands only on the basal tergites. There are 7 tergites with the seventh two-thirds as long as the sixth; the pile is moderately abundant, unusually fine and long and pale and erect.

Material available for study: The series in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Efllatoun (1945) relates that his assistant captured more than 70 males and 100 females of this strange fly in the middle of June in two wadies in Egypt. Because many were taken in copula, Efllatoun was able to establish important synonymy. All specimens were captured on the wing, over a five-day period, their flight resembling omphralids, at a height of about one meter. Always they were found at 1 to 3 p.m., the hottest part of the day.

Distribution: Palaearctic: *Mariobezzia catherinae* Efllatoun, 1945; *ebneri* Becker, 1923; *griseohirta* Nurse, 1922, *griseohirta aegyptiaca* Engel, 1933; *lichtwardti* Becker, 1913; *pellucida* Paramonov, 1929; *zarudnyi* Becker, 1913.

Genus *Acrophthalmyda* Bigot

FIGURES 18, 251, 437, 450, 797, 798, 799

Scinar Loew, Neue Beiträge II, p. 42, 1855. Type of genus: *Bombylius spheroptera* Loew, 1855, by original designation. Preoccupied by Wagl., in Reptiles, 1830.

Acrophthalmyda Bigot, Ann. Soc. Ent. France, ser. 3, vol. 6, pp. 573, 583, 1858. Type of genus: *Bombylius spheroptera* Loew, 1855, as *Cyllenia elegantula* Bigot, 1857, by monotypy.

Ostentator Jaenicke, Abhandl. Senckenberg. Naturg. Ges., vol. 6, p. 348, 1867a. Type of genus: *Bombylius spheroptera* Loew, by monotypy, as *Ostentator punctipennis* Jaenicke.

A large, peculiar fly of the general aspect of *Bombylius* Linné, but easily distinguished and recognized by the slender wing, margined and spotted with reddish sepia, on which the first posterior cell is open but narrowed and the anterior crossvein lies at the outer third to outer fifth of the discal cell. The alula is absent. Moreover, the completely opaque, reddish-brown thorax and abdomen are relatively bare; the mesonotum is

covered with sparse, fine, erect hair, and 5 stout, reddish notopleural bristles, and the abdomen is densely covered with a mat of fine, short, curled, appressed hairs in which a few, long, slender, erect, bristly hairs are intermixed. The base of the second tergite, the sides of the abdomen narrowly, and a narrow, middle stripe down the abdomen have pile of a pale brassy yellow in contrast to the remaining deep brown red pile; sides of the mesonotum likewise contrasting in color. Antennae slender and elongate; oragenal cup prominent, obliquely truncate, its walls thickened, the proboscis elongate, palpus short. Hind femur with stout bristles below; all the tibiae with spiculate bristles.

Edwards (1930) speculated as to the relationship of this fly feeling that it must somehow be related to *Marmosoma* White. It is clearly a member of the Bombyliinae; there are other genera in this subfamily with reduced alula, and far distal anterior crossvein. The spotting of veins and crossveins can be very deceptive. *Marmosoma* White does properly belong in the Toxophorinae; *Tillyardomyia* Tonnoir belongs next to *Eclimius* Loew.

An important characteristic of *Acrophthalmyda* Bigot lies in the very large, unconcealed, terminal genitalia. I believe it is necessary to place these flies in a separate tribe, the Acrophthalmydini.

While I have tentatively accepted the synonymy of *sphenoptera* Loew given by Edwards, I believe that other closely related species may be included within it. Type comparisons will be necessary to resolve this question.

After completing the following description of the strongly reddish type-species with its reddish pile, I have received two other smaller species from Chile, which are gray instead of reddish; in these the anterior crossvein is placed at the outer third of the discal cell; in other respects they are very like the type-species.

These flies are from Chile.

Length: 15 mm. including antennae; wing 14 mm.; wing spread 33 mm.

Head, lateral aspect: The head is elongate due to the strongly produced face and the extensively produced oragenal cup. The occiput is shallow, and not prominent, being only a little convex behind and sloping gradually to the eye margins which are produced outwardly much beyond the occiput. Pile of the pollinose occiput quite loose and scattered and fine, erect, of moderate length; shorter marginally. The face extends forward more than the length of the first antennal segment; it is pollinose and has numerous, but not dense, very fine, rather long, erect hairs. The eye is large, the posterior margin gently rounded, but entire, and it is longer on the upper half. Proboscis quite elongate and slender, 2 to 2½ times as long as the head, but with a short slender palpus, which appears to have a very short, fused facial segment. Front more or less flattened, with a shallow, medial depression running from the ocelli to the anterior one-fourth of the front; its

pile is scanty, fine, erect, and moderately long. The antennae are attached very near the top of the head at the upper eighth, they are relatively long and slender, the first segment is more than twice as long as wide, slightly wider than the second segment, which is about two-thirds as long as the first; both of these segments have fine, microscopic, dense, fuzz or microscopic pubescence upon them and each bears some dorsal, lateral, and ventral, long, oblique, bristly hairs, especially the first segment where the hairs are much longer and extend to the base of the segment as well. Third antennal segment longer than the first two combined, slender, slightly narrow at the base, more strongly narrowed on the apical sixth. It bears at the apex a thick, bicolor spine.

Head, anterior aspect: The head is distinctly narrower than the thorax and is not quite twice as wide as high. The head beneath the proboscis between the eyes is somewhat inflated. There are 3 or 4 furrowlike grooves running obliquely from just before the antennae to just behind the antennae. Whole front and face pollinose. The antennae are very narrowly separated, the face is moderately wider than the front of the female. The ocellar tubercle is prominent, the ocellar triangle equilateral, its pile consists of a few erect, long, coarse hairs. The oral opening is large, and relatively deep posteriorly; the lateral walls of the oragenal cup are strongly widened and inflated with fine, oblique grooves. The genae are quite narrow, the tentorial fissure deep and narrow. Sides of the face with a number of loose, scattered, rather long, fine hairs extending forward beyond the oragenal cup but absent immediately beneath the antennae. Viewed from above the head is shallowly bilobate.

Thorax: The thorax is short, slightly longer than wide, distinctly narrowed anteriorly, and very little convex. It is opaque black or sepia widely over the middle including all of the scutellum, except its lower borders, and is light pinkish brown along all of the lateral margin including the humerus and postalar callosity, and the whole of the pleuron is light reddish brown. There are 4 or 5 slender bristles on the notopleuron, several weaker bristles on the postalar callosity and the convex posterior margin of the thick scutellum has numerous, long, fine, bristly hairs. Moreover, the scutellum and mesonotum have abundant, very short, minute, curled, appressed hairs lying on the surface, copper colored on the dark areas, yellowish laterally. Dorsum of the mesonotum with fine, scattered, rather short, erect pile of a reddish color. Pile of the mesopleuron divided into a tuft directed forward along the upper margin and a tuft appressed backward on the posterior margin. In addition there is flattened, scaly pile on the sternopleuron and a dense tuft of scaly pile behind the spiracle. Squama with a wide fringe of short, jetblack, bristly hairs.

Legs: The legs are rather stout and long, the femora distinctly thickened. Anterior tibia with 7 spicules posteriorly, middle tibia with 4 rows, hind tibia like-

wise with 4 rows of spicules somewhat larger and stouter, each row with 5 or 6 bristles included. Middle femur with 1 bristle below, hind femur with 10 rather stout, ventrolateral bristles. Claws very slender, pulvilli long and spatulate.

Wings: The wings are long and unusually slender. Anterior half of the wing reddish sepia with the costal cell more yellowish brown, the demarcation behind irregular and forming spots at the forking of most veins and likewise just before the apex of the second vein, and anterior branch of the third vein. First posterior cell opened for about one-third its maximal width; medial crossvein long and oblique. Anal cell quite widely open. The anterior crossvein lies at the outer fifth of the discal cell. Axillary lobe narrow, alula absent. The area at the base of the wing and the whole of the basal cell reddish. Costal comb absent. Two submarginal cells only.

Abdomen: The abdomen is rather short, shorter than the thorax, the base is as wide as the thorax to the end of the second segment. Beyond this segment the abdomen is more or less triangular and sharply narrowed. The abdomen is opaque blackish, except the first segment, the lateral margins of all the tergites, the whole of the seventh tergite and a small confluent series of spots in the middles of other tergites, which areas are reddish brown. The pile is comparatively dense, short, curled, scaly, and glittering. This pile is coppery red on the dark areas, brassy on the posterior border of the first segment, anterior half of the second segment, down the medial row of spots, on all the lateral margins of the tergites and also includes a single row of hairs along the posterior border of the tergites. In addition, there is a considerable number of scattered, fine, erect, bristly hairs over the surface of the tergites and a few along the lateral margins. Anterior half of the first segment with a curious, dense brush of short, erect, pale yellow pile. Last sternite of the female triangular with a tuft of black pile at the apex. The male hypopygium is large and bulbous, attached in such a way as to extend directly backward; not recessed or turned downward.

The male terminalia from dorsal aspect, epandrium removed, show the figure with a very broad base and epiphallus surrounded by a wrapperlike fold on each side, and not meeting medially. The dististylus is quite stout, bean-shaped, with a short, blunt, divergent point at the apex. From the lateral aspect the epiphallus extends as a lobe dorsally above the ejaculatory process.

Material available for study: I have a female of the type-species, and have seen other examples in the collections of the British Museum (Natural History). I also have two other undescribed species lent to me by the California Academy of Sciences. These are predominantly gray pollinose.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical: *Aerophthalmyda sphenoptera* (Loew), 1855 (as *Scinar*) [= *decorata* (Rondani)], 1863 (as *Bombylisoma*), = *elegantula* (Bigot),

1857 (as *Cyllenia*), = *paulseni* (Philippi), 1865 (as *Bombylius*), = *punctipennis* (Jaenicke), 1867 (as *Ostentator*)].

Genus *Paratoxophora* Engel

FIGURES 12, 268, 460, 803, 804

Paratoxophora Engel, Occas. Papers, Rhodesia Mus., no. 5, p. 39, 1936. Type of genus: *Paratoxophora cuthbertsoni* Engel, 1936, by monotypy.

Rather small, peculiar, slender flies, which belong to the Eclimini. The occiput at vertex shows the beginnings of bilobism; the occiput laterally on the upper half of the head is more extensive but is rounded off gradually so that the head, while comparatively short, is subglobular to some extent; the eye extends farther backward below. The males are extensively holoptic with upper anterior facets enlarged and the vertical triangle and ocellar tubercle greatly reduced in size. As in *Eclimus* Loew, the antennae are slender and quite elongate, especially the first segment, which, moreover, is shaggy long pilose, particularly below. Proboscis 3 times as long as the head; face, except below the antennae, with an encircling fringe of long, silvery pile extending down along the narrow gena; sides of oragenal cup thickened above. The femora are somewhat stout, the hind pair with a few bristles below and fine, appressed scales. The tergites have a scanty row of long bristles along the postmargins; males have the hypopygium developed into 2 long, extensive, protruding, dorsal and ventral pieces, separated like the space between pincers; lower process bears the beaked dististyli. Wings hyaline, all cells open; the wing slender, the alula absent, the anterior crossvein a little beyond the middle of the discal cell; 2 submarginal cells. The general picture of this fly may be completed with the fact that it is dull black, with thin pollen or bloom, except on the shining abdomen; the latter has tufts of opaque white, appressed pile on the sides in the corners of the tergites; first segment with band of erect, golden pile.

Only a single South African species is known; it bears no relation to *Toxophora* Meigen.

Length: 6 mm. to 10 mm.; wing 5 mm. to 8 mm.

Head, lateral aspect: Head hemispherical, the occiput moderately prominent, although sloping gradually out to the eye margin, the face projects forward and is bluntly triangular. It extends below the antennae, a length 2 or 3 times that of the second antennal segment. The pile of the face forms a characteristic fringe in 1 or 2 rows on each side of the face next to the eye margin, which consists of long, almost adjacent, fine, shining, white hairs, continued all the way down the gena to the bottom of the head and it is even longer along the gena. Middle of the face without pile. Whole face pollinose. The pile of the occiput is peculiar; on the dorsal half of the head it consists of a loose fringe of some 35 or 40 very long, bristly hairs curved back-

ward. This many are found on each side and it is confined to the upper, outer portion of the upper occiput. Below on the occiput there are rather dense, shining white hairs similar to but shorter than those on the gena. Also, there is a quite wide band of dense, white pollen on the outer part of the lower occiput. Upper occiput shining and metallic. The eye is more or less hemispherical. There is a small cluster of facets dorsally and medially which is much larger than the remaining ones. Posterior margin of the eye entire. Proboscis long and slender, a little more than twice as long as the head, the labellum flat and oval, the palpus small and slender and short. The front in the males is so small it is almost nonexistent. It has a little pollen.

Antennae attached at the upper third of the head, elongate and slender and longer than the head. The first segment is extraordinarily long, at least 6 times as long as wide, the second segment is small, about as long as wide, the third segment is nearly the same width as the second segment, on a little more than the basal half, and then from lateral aspect becomes strongly narrowed. Viewed dorsally this segment is narrowest just before the middle. At the apex it bears a minute spine. The first segment is conspicuous for its long, oblique, shaggy and bristly pile on the whole outer half below, extending forward to the middle of the third segment. Dorsally on the basal half, and also ventrally, it has some short, fine, coarse, or bristly pile.

Head, anterior aspect: The head is a little wider below than above, dominated by the extensive eyes, the enlarged facets show from in front. The head is distinctly wider than the thorax, the eyes meet in the middle from close to the antennae to the small, scarcely raised ocellar tubercle. This tubercle is an equilateral triangle with small ocelli but with a tuft of 4 or 5 long bristly hairs curled forward. The antennae are nearly adjacent at the base, the oral opening is small and triangular and deep behind; its anterior walls are covered with white micropubesence and are curiously inflated and widened anteriorly and narrowing posteriorly. There is a medial fissure on the face beneath the antennae. The genae are narrow and set off by a shallow fissure. From above the postvertex is shallowly bilobate with a shallow fissure.

Thorax: The thorax is elongate, rather compressed laterally, gently arched, the scutellum large and triangular, the mesonotum more or less shining black with bluish reflections and a thin pollen. It is covered with loose scattered, moderately long, erect, shining hairs. Notopleuron with 2 black bristles. Scutellar disc with similar hairs and the margin with a few longer, slender black hairs. Pleuron entirely gray pollinose, the mesopleuron dorsally and posteriorly with much long, fine, tufted white pile. Hypopleuron, pteropleuron, and metapleuron bare. Squamal fringe fine and loose and not very dense. Prothorax no more extensive than in most bombyliids.

Legs: The femora are relatively stout; tibiae and tarsi more or less short but more slender. Anterior

tibia with very fine, short spicules, 3 or 4 in each of 3 rows. Middle tibia with 5 or 6 longer stouter spicules in 4 rows. Hind tibia with fewer spicules in 4 rows but they are stouter and longer, most rows with not more than 3 spicules. Hind femur with 3 rather long, stout bristles ventrolaterally, and with dense, minute, short, flat-appressed, iridescent red and green scales, which give way to white scales on this femur as well as the first 4 femora. Base of all femora narrowed slightly. Claws long, sharp; the pulvilli long but quite slender.

Wings: The wings are hyaline, comparatively large, quite slender, especially toward the base. There are 2 submarginal cells. All the cells widely open including the anal cell. The anterior crossvein lies just before the outer fourth of the discal cell. Axillary lobe narrow, alula absent, ambient vein complete.

Abdomen: The abdomen elongate and slender, somewhat compressed laterally, the first two segments are as wide as the thorax and the abdomen is slightly narrowed beyond, more narrowed on the last three segments, and these segments are more strongly compressed. First segment opaque, greenish pollinose with a dense and complete band of rather long, erect, coarse, brassy yellow pile, that changes to long white hairs laterally. Other tergites black, feebly shining with two kinds of pile. Along the posterior margins laterally there are bands or tufts of appressed opaque whitish, somewhat flattened pile, rather matted. Then each tergite has across the middle on the posterior margin less developed on the apical tergites, a fringe of long, slender, black bristles and bristly hairs. They are especially prominent on the fifth to seventh tergites. I find in the male 8 tergites, the last two subequal in length. The hypopygium consists of the ninth tergite and sternite, and it forms a curious, elongate, prominent, laterally compressed beak-like process which has upper and lower valves with a wide gap between. The dorsal component has a fringe of scattered bristly hairs ventrally, the ventral component is divided in the middle. It appears to bear the deep apical segment on each side apically, and has the aedeagus in the middle. Last sternite with considerable fringe of black bristly hairs apically.

The male terminalia from dorsal aspect, epandrium removed, show a very complex structure. The basistylus shows extensive, dorsal membranous areas, which however, are connected and bridged in the middle. The epiphallus and ejaculatory ducts actually arise basally, are turned backward behind the epandrium, and then turn downward as an extremely long, slender, ventral tube. The dististyli are rather curious, long, slender, with odd commalike lobes that turn out apically. It is bilobed, and in the middle visible both dorsally and laterally in what appears as a long tonguelike extension of the basistylus, where one normally finds the epiphallus. This curious condition of an extremely long, slender, coiled, and curved ejaculatory tubelike process has been duplicated and certainly evolved independently in *Amictus* Wiedemann. In *Amictus* the ejaculatory process is also produced from the back part of

the hypopygium and turns forward; it runs between the basistyli. The dististyli are larger, with an inward, curved hook at the apex and from the lateral aspect there is a well-developed stout, upwardly curved spout-like epiphallus. The epandrium is quite different from *Paratoxophora* Engel. It has a prominent dorsobasal lobe extended backward, and in front a posteroventral lobe. Cerci arise dorsally at the top of the structure.

Material available for study: A pair of the type-species received through the kindness of Dr. A. J. Hesse of the South African Museum, Capetown.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no comment upon the adults.

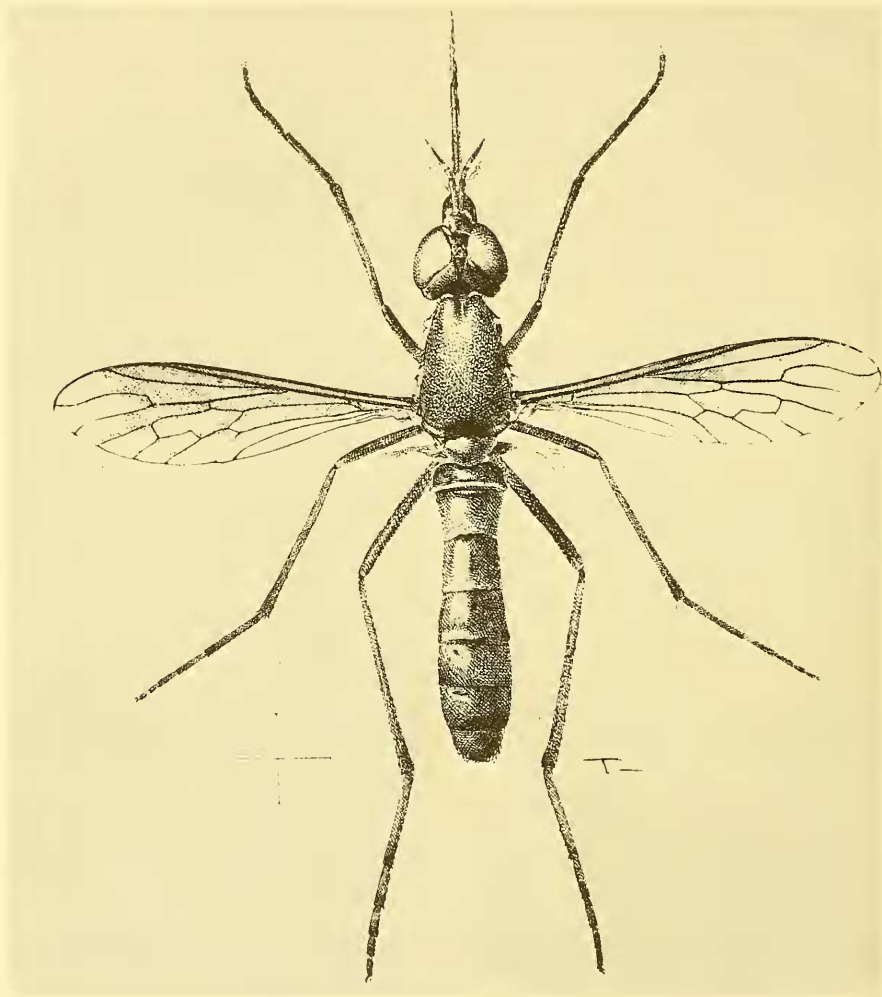
Distribution: Ethiopian: *Paratoxophora cuthbertsoni* Engel, 1936.

Genus *Eclimus* Loew

FIGURES 15, 258, 454, 572

Eclimus Loew, Stettiner Ent. Zeitung, vol. 5, p. 154, 1844. Type of genus: *Eclimus perspicillaris* Loew, 1844. Designated by Coquillett, p. 536, 1910, the first of 2 species.

Eclimmus Verrall in Scudder, Nomenclator Zoologicus, p. 118, 1882.



TEXT-FIGURE 23.—*Eclimus gracilis* Loew, after Austen.

Engel (1933), p. 55, key to several Palaearctic species.
 Maughan (1935), p. 68, key to 3 Utah species.
 Hull (1965), pp. 95-97, new western species.

Small, slender flies of blackish coloration characterized by the fact that the wing is very slender and much narrowed at the base. The alula is absent, the axillary cell is very narrow and long, the anal cell very widely opened even more so than the width of the axillary lobe. The wing is dark brown with large but diffused windowlike spots in the 4 posterior cells, the discal, and the apex of the second and third basal cells. The legs are relatively long and slender, the abdomen hemicylindrical, and both thorax and abdomen covered only with microscopic, relatively sparse, appressed setae, each arising from a subtuberculate base, which gives the abdomen and thorax a rugose appearance. Also, the head is quite elongate, the eyes are carried forward, the oragenal area is very extensive, slanted forward with long slender proboscis and long filiform labellum, and a conspicuous 2-segmented palpus which is almost as long as the antennae. The third antennal segment is blunt at the apex, from above the head is semibilobate but there is no cavity. They are almost mosquito-like in appearance except for the spotted wings.

Austen (1937) gives a full complete figure of *Eclimus gracilis* Loew.

These flies are known only from two species found in southern Europe.

Length: 7 mm. excluding the proboscis; 9 mm. including the proboscis. Wing: 5 mm. in length.

Head, lateral aspect: The head is large, especially the eye. The extensive face and oragenal area are slanted forward and almost conical leaving also a very extensive gular area beneath the eye; this wide, shining gular area bears a number of extremely fine, long, dark, downturned hairs, which are therefore erect. The face and the extensive oragenal comb or cup are polished and shining and bare. The gena proper is absent as the eye margin extends quite to the oral cup. The occiput has a clump of rather stiff, blackish, erect bristly hairs on each side situated rather low and opposite the humerns, giving way to more slender pile below. From above the eye is rather strongly and diagonally excavated leaving the dorsal eye profile triangular. The front in the male has a transverse depression nearly midway between the antennae and ocelli. The whole upper part of the front is flat and granulated.

Head, anterior aspect: Ocellar tubercle large but low; the proboscis is $1\frac{1}{2}$ times as long as the maximum head length. The second segment of the palpus is flattened, leaflike, large, conspicuous, twice as wide at the base as at the apex. Second and third antennal segments slightly longer than the slender first segment. First segment rather widely separated at the base. The third segment is blunt apically. The apical part of this segment is scarcely wider than the base.

Thorax: Thorax much more narrow than the head, elongate, high, with parallel sides; at most the mesonotum is very gently convex but a little more convex

posteriorly. It is blackish in color, strongly shining, with the pleural sclerites rather reddish-brown centrally. Whereas on the mesonotum and scutellum the microsetae are dense, they are relatively quite sparse on the pleuron, and are confined to the upper metapleuron, upper sternopleuron, and the hypopleuron above the posterior coxae. The hypopleuron above the middle coxae, all the anterior sternopleuron and all the pteropleuron are quite bare, polished and shining. The metapleuron appears to be much reduced in size and is bare with a yellowish spot ventrally; however, there is a small bullose area behind the wing and above the haltere, which is microsetate, and which appears to be metapleuron rather than metanotum. Squama extremely short.

Legs: The legs are quite slender and elongate, especially the hind pair. The slender hind femur is at least $1\frac{1}{2}$ times as long as the anterior femur, however, the anterior coxae is unusually long and slender, fully three-fourths as long as the anterior femur itself. The anterior tibia has numerous oblique, short, setae along the anteroventral margin, and some scattered bristly setae posteriorly. The anterior femur has a few quite long, very slender, erect, ventral, stiffened hairs. Middle femur with a few short, fine hairs ventrally. Hind femur, however, with only very sparse minute appressed setae, placed principally along the lateral margin. Hind tibia even a little longer than the femur, very slender with a few, fine, oblique bristles, not more than 5 in any row, and there are 4 rows. Tarsi extremely slender, the claws fine, scarcely curved at the apex, the pulvilli large.

Wings: The wings are comparatively wide and apically rounded, but remarkably slender and narrow on the basal half. The axillary lobe is very long and slender, the alula absent, the ambient vein complete, the wing fringe long, fine, and dense. The general coloration is rather dark brown but there are large, clear, yet diffusely margined windowlike spots in all of the posterior cells, middle of the discal cell, and apex of the second and third basal cell. Anal cell very widely opened. There are 2 submarginal cells. The anterior branch of the third vein rises abruptly in a rounded arch.

Abdomen: With parallel sides, elongate, hemicylindrical, with 7 tergites visible above, and with the second through the fourth of equal length. The abdomen is largely blackish, the first segment and postmargins and lateral margins of the other segments dark reddish-brown. The abdomen is everywhere shining, rather densely microgranulate with appressed blackish microsetae. All of these tergites have a shallow transverse depression, including the first tergite; they are continuous across the surface.

Material available for study: One female of *Eclimus gracilis* Loew which, because the spotting is somewhat different from the illustration given by Engel, I believe is probably a subspecies.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic: *Eclimus gracilis* Loew, 1844, *gracilis festae* Bezzi, 1924; *perspicillaris* Loew, 1844.

Genus *Thevenemyia* Bigot

FIGURES 16, 19, 248, 249, 422, 563, 795, 796

Thevenemyia Bigot, Bull. Soc. Ent. France, ser. 5, p. clxxiv, 1875a. Type of genus: *Thevenemyia californica* Bigot, by monotypy.

Thevenemyia Bigot, 1875, lapsus.

Thevenemyia Bigot, Ann. Soc. Ent. France, ser. 7, vol. 2, p. 339, 1892.

Epibates Osten Sacken, Bull. U.S. Geol. Survey, vol. 3, p. 268,

1877. Type of subgenus: *Epibates funestus* Osten Sacken, 1877. Designated by Coquillett, p. 538, 1910, the first of 7 species.

Arthroncurea Hull, Ent. News, vol. 77, p. 226, 1966. Type of subgenus: *Eclimus tridentatus* Hull, 1966.

Engel (1933), p. 55, key to several Palaearctic species.

Hall (1969), pp. 12-19, key to 36 world species.

These very distinctive flies have a slender form, with elongate antennae and abdomen, and in some species they are much more slender than in others. The thorax is at most only slightly humped or arched, the abdomen is not decumbent, the head is slightly decumbent in some species, and no scales are present. The proboscis also varies very considerably; it may be 6 times as long as the head or scarcely more than equal the length of the head. The face is shining with some pile or occasionally pollinose with considerable pile; the oragenal cup, however, is large, moderately deep below but filled by a sloping expansion on the upper half and this odd, upper, enclosed part bears a number of long, slender hairs. The oragenal cup may be moderately or may be quite extensively produced; the gena is reduced until it is almost absent. The first segment of the elongate antenna is 2 or 3 times the length of the second; the third is longer than the first segment, gradually and slightly attenuate to the obliquely truncate apex. Pile of first segments varying in length but never long. The tibiae are spiculate, the hind femur has a few short bristles or almost none. The general coloration of these flies is black, shining in some species, dull in others. In some species the mesonotum is nodose spinose in males (subgenus *Epibates* Osten Sacken).

Wings hyaline or with the veins strongly tinged or set out in confluent black margins. All cells are open, the anal cell narrowly, the first posterior cell maximally. The anterior branch of the third vein may be strongly sigmoid or sometimes straight, arising especially abruptly at its base. Male costa sometimes spinose. In *Thevenemyia* Bigot the occiput is very slightly bilobate above. I doubt it is closely related to the Cylleninae; I believe it is more probably an aberrant member of the Bombylinae. In either case I place it in the tribe Eclimini with *Tillyardomyia* Tonnoir.

The American genus *Thevenemyia* Bigot can readily be distinguished from the European *Eclimus* Loew—

of which only 2 species are known—by the strongly narrowed base of the wing in *Eclimus* Loew and also by the curious, much extended, slanting extension of the face and oragenal cup. Also by the type of vestiture which is very minute and short.

Thevenemyia Bigot, while represented by 2 species in the southern Palaearctic region, finds its real home in the western half of the Nearctic area. Several species have been described from Australia (not seen by the author), and one from New Zealand.

Length: 7 mm. to 17 mm.; wing 8 mm. to 13 mm. Proboscis sometimes as much as 9 mm.

Head, lateral aspect: Head is subglobular with both face and oragenal cup extensive but sharply truncate or plane and the oragenal cup receding backward from the lateral aspect. In some individuals the face and oragenal cup are two-thirds as long as the eye. The occiput is prominent, more so in females than in males. The face is polished and bare, except sometimes narrowly pollinose across beneath the antennae and in some species wholly pollinose. It may be totally without pile or have a long fringe of fine hairs projecting forward to the anterior edge. Likewise in some species with pollinose face, they may be covered throughout with rather dense, erect, long, fine pile extending down over the whole of the oragenal cup. In most species the oragenal cup is bare, polished and shining. The occiput bears a rather deep-set, medial, central fringe of long, coarse hairs in several rows, leaving only short, minute setae outwardly, or the entire occiput may be covered with long, fine or coarse pile, becoming shorter toward the margin of the eye. Ventral pile beneath the head and occiput long and fine, either loose or rather dense. The eye is more or less hemispherical, extended outward well beyond the posterior margin which is entire. The eye is large, extending to the bottom of the head, the upper facets slightly enlarged and the eye more or less flattened dorsally.

The proboscis in some species is short and stout with long, flattened, oval, grooved labella which is very little longer than the head in length; here the palpus is half as long as the proboscis, and its second segment is short and lanceolate. In some species the proboscis may be 4 or 5 times as long as the head; in these species the palpus is long and slender, including the distal segment, but no more than one-fifth as long as proboscis; palpal pile always short, and fine and erect. The antennae are attached closely adjacent at the upper sixth of the head. The antennae are elongate and slender with the first segment from 3 to 5 times as long as wide; the second segment from 1 to 1½ times as long as wide; the third segment is as wide at the base as the second segment and gradually tapered to the blunt apex, which may have a minute microsegment. The first segment has either sparse, subappressed setate hairs below and shorter ones above or has rather long, shaggy pile both dorsally and ventrally; second segment with very short, fine setae; the third segment near the apex sometimes has 2 or 3 fine hairs about as long as the segment is wide.

Head, anterior aspect: The head is about $1\frac{1}{2}$ times wider than high, or a little more. The eyes are in contact for a distance approximately equal that of the front, or they may be separated as in *Thevenemyia celer* Cole by not more than half the width of the ocellar tubercle. The antennae are separated at the base by about half the width of the first segment, or in some instances more than the width of the first segment. The ocellar tubercle is small, and from the front is more protuberant than it is laterally, since on each side the eye is raised above the vertex. The ocelli are large, lie adjacent to the eye, and form either an equilateral or short isosceles triangle. The ocellar triangle bears a tuft of fine, black, bristly hairs of varying number, sometimes rather long and sometimes short.

The front is small and triangular in males but flattened across the middle, and in females with a large shallow depression; it is either without pile or with a tuft of short, bristly hairs on each side posteriorly toward the vertex. It is with or without pollen, with or without a transverse groove in the male, and with or without a medial groove. The front in the female has much long, fine, more or less erect pile. The oral opening is either short or long oval, quite deep, except in the middle anteriorly which has an odd, polished, somewhat convex, liplike plate in all species. In a few species this plate is pollinose, and even bears pile anteriorly. The walls of the oragenal cup are knife-sharp and thin and the gena is quite narrow and linear; the tentorial fissure is likewise narrow. Viewed from above the occiput is at most slightly bilobate; it slopes from the swollen interior gradually to the eye margin and sometimes it slopes to the level of the eye or beneath it before reaching the margin, leaving a very distinct vertical rim around the upper part of the eye. Also, ventrally there is, in at least some species, an odd, lobelike bulla placed on each side below the foramen.

Thorax: The thorax is elongate, narrow, compressed laterally, convex when viewed from front or rear, and only very gently convex from the side. The prothorax is distinctly lower than the mesonotum and is much shorter than in *Lepidophora* Westwood and bears a few fine hairs dorsally, a few others laterally. The mesonotum is usually either dull or shining black and may be almost opaque. The pile varies from short, bristly, though fine, mostly subappressed, more nearly erect on the posterior half to others, like *Thevenemyia lotus* Williston, which have two types of pile, short, subappressed, somewhat scaliform golden pile along the whole lateral margins and in front of the scutellum and on the scutellum, and with the dorsum containing mostly erect, numerous, very fine hairs, rather long and becoming still longer on the scutellum. The notopleuron has 3 or 4 strong bristles, either black or pale. The scutellum is thick, convex and large. The mesopleuron has much long, appressed pile in some species, but more scanty, fine hairs and bristly pile in other species which leave this area nearly bare; metapleuron in front of haltere bare, below and behind spiracle with tuft of

long pile. Pteropleuron and hypopleuron bare. The sternopleuron has considerable pile and there is a dense, abundant patch of pile situated posteriorly and ventrally to the spiracle. The metanotum has a large, conspicuous patch of long, fine, or bristly pile covering the whole surface; halteres quite large; squamal fringe generally scanty, sometimes in only 1 or 2 rows, sometimes forming a dense, wide border.

Legs: The legs are long and comparatively slender, the hind femur a little more stout or thickened; anterior tibia with 5 minute, slender spicules ventrally, other species with an additional row of 6 posterodorsally. Spicules of middle tibia also weak; on the hind tibia they are short and slender and lie in 4 rows, the ventro-medial row contains 7, the dorsomedial row contains 9, the anterodorsal row and the anteroventral row contain only 2 or 3. The hind femur has at most 2 or 3 small, sharp, oblique spicules and sometimes with none; the pile is entirely setate and flat-appressed; the anterior 4 femora sometimes have considerable loose, long, fine, erect pile on most of the ventral side. Also in some species like *Thevenemyia lotus* Williston the pile, instead of being setate, consists of dense, slender, flat-appressed, whitish, scalfiform hairs. The claws are short, comparatively stout, strongly curved at the apex with long, spatulate pulvilli. In all species the anterior coxae are unusually long.

Wings: The wings range from hyaline, with the costal cell darkened to more commonly with all the veins margined with brown, sometimes widely, so that the whole wing appears to be more or less tinted. The wing is elongate, the anterior and posterior margins for the most part parallel-sided, and in the males of some species the apex of the wing anteriorly is rather strongly arched backward. Males generally have a double row of tubercles, small or large extending along the costa from the base of the basal cell to or close to the end of the marginal cell. There are 2 submarginal cells and 4 posterior cells with the anal cell open. The anterior branch of the third vein arises abruptly and sometimes even at a right angle, leaving the second submarginal cell very strongly arched at the base and the anterior branch vein sigmoid. The wing of *Thevenemyia* Bigot is a little peculiar in the strong tendency for the anterior crossvein to be shortened pulling the third vein down toward the fourth and both second and third vein at this point may be somewhat thickened. The intercalary vein is often rectangular, and the anterior crossvein lies at the middle of the discal cell. The axillary lobe is relatively narrow, the alula varies from narrow to almost absent as in *Thevenemyia lotus* Williston; ambient vein complete.

Abdomen: The abdomen is decidedly elongate, subcylindrical with the sides nearly parallel and sometimes even compressed laterally. The ground color varies from opaque to shining black. The pile varies from species that have shining, curled, appressed, metallic, somewhat scalfiform pile to which may be added moderately numerous, scattered, fine, erect hairs which tend to

become longer and more conspicuous laterally, to other species of this genus in which the appressed tomentum is lacking. The pile toward the end of the abdomen may in some species become coarse hair or even fine bristles. Some species have conspicuous postmarginal bands of paler pile on the tergites. Sternites are nearly bare or sometimes rather densely pilose. I find 9 tergites in both males and females. In the females the last 2 tergites are short, recessed with a posterior border of short, stout spines. The dististyli of the male terminalia turn upward at apex of abdomen or extend backward.

The male terminalia from dorsal aspect, epandrium removed, show an oval figure with very large, basally stout, convergent dististyli which are pointed at the apex. In the lateral aspect the epandrium is almost exactly like that of *Sparnopolius* Loew. It has a short, comparatively sharp lobe basally both above and below, and the shape is very similar. The epiphallus is similar but considerably shorter. The ejaculatory process ends quite near the middle. There can be very little doubt these flies belong in the subfamily Bombyliinae, where I have erected a separate tribe for them.

Material available for study: I have before me about 10 species from western North America, and 1 from Mississippi.

Immature stages: Jack Hall, University of California at Riverside, California, recalls having obtained adults of one species from pupa emerging at the holes of anobiid beetle larvae from pieces of deadwood found in that area, and more recently he has obtained a definite record of the flies parasitizing a cerambycid beetle (see life histories).

Ecology and behavior of adults: The ecology of the adults of *Thevenemyia* Bigot is interesting. Various authors have noticed the strong tendency on the part of these flies to hover around the bark of dead trees and to some extent around burnt-over trees.

The rare Mississippi *Thevenemyia* sp. I have never associated with flowers; all others I have collected have been western flower-visiting species; one small species *Thevenemyia culiciformis* Hull was abundant in August in woodland on tall composites like iron weed in Patagonia, Arizona; these flies like *Geron* species bobbed up and down above flower heads before settling down, where because of their small size, long legs, etc., and long slender proboscis they appeared much like giant mosquitoes; the same species also visits low-growing desert flowers.

Distribution: Nearctic: *Thevenemyia californica* Bigot, 1875; *celer* Cole, 1919; *culiciformis* (Hull), 1965 (as *Eclimius*); *funesta* (Osten Sacken), 1877 (as *Epibates*); *hulli* (Hull), 1965 (as *Eclimius*); *harrisi* (Osten Sacken), 1877 (as *Epibates*); *harrisi* Johnson, 1914; *laniger* Cresson, 1919; *leechi* Hall, 1954; *lotus* Williston, 1893 [= *auratus* Williston, 1893]; *lucifer* (Osten Sacken), 1877 (as *Epibates*) [= *auripilus* (Bigot), 1892 (as *Amictus*), = *lucifer* Aldrich, 1905, lapsus]; *maculipennis* (Hull), 1965 (as *Eclimius*); *magna* (Osten Sacken), 1877 (as *Epibates*) [= *melano-*

pogon Bigot, 1892]; *marginata* Osten Sacken, 1877; *melanosa* Williston, 1893; *muricata* (Osten Sacken), 1877 (as *Epibates*); *nigra* (Macquart), 1834 (as *Apatomyza*) [= *aegiale* (Walker), 1849 as *Cyllenia*]; *ostensackenii* (Burgess), 1878 (as *Epibates*); *sodalis* Williston, 1893; *tridentata* (Hull), 1966 (as *Eclimius*), (subg. *Arthronoeura*); *yosemite* Cresson, 1919.

Neotropical: *Thevenemyia auripilus* Osten Sacken, 1887; *fascipennis* Williston, 1901; *halli* (Hull), 1965 (as *Eclimius*); *quadrata* Williston, 1901.

Palaeartic: *Thevenemyia hirta* Loew, 1876; *quedenfeldti* (Engel), 1885 (as *Epibates*); *venosa* Bigot, 1892.

Australian: *Thevenemyia furvicostata* Roberts, 1929; *longipalpis* Hardy, 1922; *nigrapicalis* Roberts, 1929.

Hall (1969) described the following new species from the United States: *accedens*, *affinis*, *canuta*, *melanderi*, *notata*, *painterorum*, *phalantha*, *speciosa*; and from Australia: *australiensis*, *mimula*, *tenta*.

Genus *Tillyardomyia* Tonnoir

FIGURES 17, 250, 440

Tillyardomyia Tonnoir, Rec. Canterbury Mus., vol. 3, p. 101, 1927. Type of genus: *Tillyardomyia gracilis* Tonnoir, 1927, by monotypy.

Relatively slender, medium-sized flies that are readily recognized by the subglobular head and its elongate antenna, together with the patterned, slender wing with 3 submarginal cells, reduced anal area, no alula, and with the odd shape of the second and third posterior cells and discal cell. These flies are related to *Eclimius* Loew in the general form of the head and the quite elongate, shaggy-haired first antennal segment; the third segment is less narrowed and is more spear-shaped, and the occiput is more prominent above. These flies bear straggly, scattered, coarse hairs and stout notopleural bristles.

The only species known is from New Zealand.

Length: 10 mm.

Head, lateral aspect: The head is globular, the appearance heightened by the extensive and tumid occiput which is especially protuberant above, bilobate, and creased in the middle behind. The antennae are set quite low at the middle of the head, hence the face is not very high and extends but little beyond the eye margin. The oral opening is large and extensive, becoming wider below and behind. The proboscis is moderately slender, the apex dilated and leaflike, and the whole perhaps $1\frac{1}{2}$ times as long as the head. The palpus is quite long and slender with narrowed, spatulate apex which appears to be a separate segment. There is also some slight indication that there may be an extremely short basal segment, making 3 segments. First segment of antenna elongate, pilose on all sides, the pile is dense, bushy and black, and longer laterally. The face is bare and shining along the epistoma, shining below the antenna. The occiput has dense, coarse, bristly pile that is rather long, especially above, black,

and mixed with some slender black bristles; lower occipital pile fine, long, erect, delicate and white.

Head, anterior aspect: The ocellarium is moderately high with a tuft of long, bristly hairs or slender bristles in the middle. The sides of the front bear numerous, quite long, slender, black bristles leaving the medial part bare, the bristles divergent, and the bristles give way below on each side to a tuft of rather dense, shorter, whitish pile.

Thorax: The thorax is gently arched, mesonotum largely bare with scattered, long, coarse hairs anteriorly, especially across the anterior margin. These hairs are black. There is coarse, opaque, mostly white, mostly appressed, rather straggly pile and hairs on humerus, the lateral margin of the mesonotum, the posterior margin of the scutellum, the upper half of the mesopleuron and a dorsal patch on the sternopleuron. Some of the pile on the upper part of the mesopleuron extends outward, and there is a conspicuous tuft of similar, more or less erect, opaque whitish pile on the sides of the metanotum and on the metapleuron, in both places extensive and abundant and also a small patch in the extreme posterior corner of the hypopleuron. The basal half of scutellum has rather numerous, appressed, flattened, or scalelike black hairs and some similar very scanty hairs on the mesonotum. The notopleuron has 3 conspicuous, quite stout, black bristles; lateral postmargin of the scutellum with 3 pairs of slender, long, black, bristly hairs.

Legs: The legs are rather slender, the femora and tibiae with pale scales; anterior tibiae with 3 or 4 moderately stout, spinous bristles posteriorly; bristles of middle tibiae more conspicuous.

Wings: The wing is relatively slender and the axillary area much reduced and narrowed; there is no alula. There are 3 submarginal cells with the first almost quadrate and the apex of the marginal cell greatly widened, its end nearly truncate. The discal cell is greatly narrowed on the distal half due to the strong forward bend or curve of the third posterior cell tending to occlude the discal cell. The anterior crossvein is near the outer fifth of the discal cell. Anteriorly the wing is rather sharply sepia brownish or blackish, the black color filling basal half of the second basal cell obliquely, all of first basal cell, basal half of second submarginal cell, bordering it anteriorly and distally, and filling all of the first submarginal cell, except the middle and posterior margin, and filling the apex of the wing. There are 4 posterior cells and the anal cell rather widely open.

Abdomen: The abdomen is subcylindrical with nearly parallel sides; it is almost bare but with some rather abundant, black, appressed, slender scales or scalelike hairs on the first two tergites and less abundant, similar hairs on the sides of the remaining tergites. Some of the flattened pile along the sides of the abdomen is white. Probably the entire abdomen is covered in fresh specimens. Apex of abdomen obliquely truncate, the height increased at the apex because of a certain amount

of lateral compression. The interior of the apex of the abdomen is densely filled with matted, long, fine pile, so that the terminalia cannot be inspected without dissection.

Material studied: A female of the only known species kindly lent me by Dr. R. H. Painter.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Australian: *Tillyardomyia gracilis* Tonnoir, 1927.

Genus *Crocidium* Loew

FIGURES 57, 58, 59, 327, 526, 528, 840, 841, 842

Crocidium Loew, Öfvers. Kongl. Vet. Akad. Förhandl., vol. 17, p. 85, 1861. Type of genus: *Crocidium pocclopterus* Loew, 1860, by monotypy.

Paramonov (1931a), p. 182, treatment of Palaearctic species. Hesse (1938), pp. 788-792, key to 11 South African species. Efflatoun (1945), pp. 126-127, key to 2 Egyptian species.

Small, slightly humped, blackish flies, characterized by a conically elongate and more or less tapered and laterally compressed abdomen, which is slightly decumbent. Superficially they resemble the genus *Geron* Meigen. These flies, however, are properly related to the Bombyliinae and, together with *Apatomyza* Wiedemann and *Adelogenys* Hesse, form a rather special group. Overlying the dark ground color there is rather abundant, long, erect, delicate white pile. These flies are a characteristic element of South African fauna. The species fall into two groups, one of which has unspotted hyaline or milky tinted wings, much longer proboscis, longer first antennal segment, the third segment more slender, bare and shining front. The second group has more or less opaque, tinted wings with distinct spots or clouds on crossveins, or bands broken into spots. Front and face dull rather than shining; proboscis shorter and stouter. First antennal segment shorter, that is, much less than 3 times as long as the second. In *Crocidium* Loew the 2 submarginal cells and the anterior branch of the third vein end at the wing apex, in contrast to *Gonarthrus* Bezzi. The thorax is a little arched, but this appearance is merely heightened by the somewhat decumbent abdomen. *Apatomyza* Wiedemann is separated by its very long first and long third antennal segments and both this genus and *Adelogenys* Hesse have, in contrast to *Crocidium* Loew, a more arched thorax and a much longer, more compressed and therevid-like abdomen in appearance. Genae in *Crocidium* Loew distinctly developed, in contrast to *Adelogenys* Hesse where it is absent or virtually so.

Crocidium Loew is a South African Group of flies with 2 additional species in Egypt.

Length: 3 to 6 mm.

Head, lateral aspect: The head is rather subquadrate in profile, the front and the moderately extended face are more or less flattened and also in profile

there is little or no occiput visible on the upper half of the eye, although it is comparatively tumid on the lower third of the eye. The genal region is wide and sometimes exceptionally broad; in the very wide species apt to be a little swollen and protrusive. The face is moderately developed, angularly produced since the face is flat and makes a right angle with the low, large, thin walled, sometimes shallow, sometimes deep, obliquely truncate, retreating oragenal cup. The middle of the face is sharply and angularly demarcated from the lateral portion of the face. This middle portion, which reaches to the base of the antenna and is shining, polished and bare, might be regarded as a dorsal extension of the oragenal cup. The lateral face has considerable exceptionally fine, long, erect, delicate, silvery white hairs, which continue to extend over the whole of the wide gena and the ventral occiput. The surface of this area is pollinose. The occiput is without central cavity, but viewed from above each lateral half is slightly convex. The postvertex itself is triangular and a little convex and delineated by lateral creases. Palpus quite fine and slender, apparently of 3 segments, the third quite short; 2 segments are certainly present. Proboscis long and slender and 3 or 4 times as long as the head. Antenna attached near the upper third of the head, elongate and slender, the segments all of about equal width. The first segment varies from at least 3 times as long as the rounded, beadlike second segment to barely more than twice as long.

It bears a few fine hairs. The third segment is nearly twice the combined length of the first 2 segments, slightly narrowed near the apex and with a small, spine-tipped microsegment.

Head, anterior aspect: The head is considerably wider than the thorax. In the male the eyes touch, although for a very short distance, or in other species narrowly separated; they are quite broadly rounded medially so that there is quite a narrow, posterior extension of the front; upper facets of male enlarged. Female eyes may be separated by as much as one-third the width of the head. The front, except for this extension, is quite small and tubercle, flattened, with pollen but no pile. The ocellar tubercle is low; the ocelli are small and in the male situated on or almost at the eye margin. The front is separated from the face by a faint diagonal crease: it is not flattened and sunken in either male or female as in *Phthiria* Meigen. From in front the head is broadly oval, and because of the exceptional width of the gena the genofacial space is widely divergent below and viewed as an angle with the front it forms at least a right angle. Oral opening with straight sides, slightly widened toward the proboscis.

Thorax: The thorax is gently convex, distinctly longer than wide and with numerous, long, somewhat flattened, more or less erect, silvery white hairs. There are no differentiated bristles, except that possibly some of the longer hairs on the rounded rim of the rather thick and convex scutellum may be regarded as slender bristles. Mesonotum and pleuron pollinose; meso-

pleuron with a few, long, scattered hairs; metapleuron bare; hypopleuron with a few hairs.

Legs: The legs are weak. There are no ventral spines on the femora; a rather long apical spur is below upon the middle tibia. The spicules upon the tibiae are longer, and better developed and more conspicuous than in *Phthiria* Meigen.

Wings: The wings are broad at the base, hyaline or milky tinted in one group, clouded or spotted. There are 2 submarginal cells, the second is rather narrow for the anterior branch of the third vein is barely convex. There are 4 posterior cells, all of them quite widely open. The anal cell is closed with a rather long stalk; the axillary lobe is quite large, and the second anal vein quite straight. The anterior crossvein enters the discal cell at the middle or in some species at the outer fourth; the upper intercalary vein is about one-third as long as the medial crossvein. The costal cell is expanded basally; base of costa dilated and with prominent setae; ambient vein complete, the alula of no great width.

Abdomen: The abdomen is elongate but only about $1\frac{1}{2}$ times as long as the thorax, but strongly tapered and even, somewhat compressed laterally. The tergites have numerous, exceptionally long, quite fine, erect hairs, generally silvery white; they also have some appressed, comparatively broad scales or scaly hairs. Sternites likewise with dense, quite long, erect, white pile growing shorter toward the apex of the abdomen. Eight tergites visible dorsally. Female hypopygium with 3 or 4 pairs of spines. Male hypopygium formed of 2 large, adjacent, mammiform or convex, hoodlike plates turned downward from a dorsal position, and in Egyptian species with on each side a stout recurvate spine.

Hesse (1938) says of the male terminalia:

... the hypopygium is without a long lobe-like process at the base of the basimeres, yet with a distinct process present; dististyles (beaked apical segments) either slender, elongate, cylindrical, sparsely pilose, acutely pointed, or flattened and twisted; aedeagus well developed, without ventral process, joined onto the basal parts by a flange or flap-like ramus; lateral struts either strongly developed, elongate and directed outward or much shorter and directed obliquely downward or towards the base; basal strut racquet-shaped.

The male terminalia from dorsal aspect, epandrium removed, show long, nearly straight attenuate, apically pointed dististyli. What appears to be the aedeagus is long and slender, reaches to the base of the dististyle; it overlies a broader structure arising from the ramus, and deeply divided for nearly two-thirds of its length, and emits 2 long, slender, slightly curved processes of the same thickness as the ejaculatory process. This structure corresponds to the lateral divided claspers in *Phthiria* Meigen. The epandrium is rather similar to that of *Phthiria* Meigen and the basal apodeme similar and large. All of this may indicate a relationship between *Crocoidium* and the *Phthiriinae*. There is a slender bridge from the ramus on each side slightly reminiscent of *Phthiria* Meigen. The base of the aedeagus is large and egg-shaped. From lateral aspect, the large basistyle

is bowl-like, widening basally, with the dististyle conspicuous and slightly curved.

Material available for study: The series in the British Museum (Natural History) and 3 species kindly sent by Dr. Hesse for dissection and study.

Immature stages: Unknown.

Ecology and behavior of adults: Eflatoun (1945) records capturing a considerable series of *aegyptiacum* Bezzi upon flowers of *Calendula* and other bright colored composites.

Distribution: Palaearctic: *Crocidium aegyptiacum* Bezzi, 1925; *nudum* Eflatoun, 1945.

Ethiopian: *Crocidium chrysonotum* Hesse, 1938; *costilabre* Hesse, 1963; *dasypolium* Hesse, 1963; *depressifrons* Hesse, 1938; *dichopticum* Hesse, 1963; *immaculatum* Bezzi, 1922; *karoanum* Hesse, 1938; *lactipenne* Hesse, 1963; *leucostomum* Hesse, 1963; *melanopalis* Hesse, 1938; *microstictum* Hesse, 1963; *namaguense* Hesse, 1963; *nigrifacies* Bezzi, 1921; *nitidilabre* Hesse, 1938; *pachycerum* Hesse, 1963; *phaenochilum* Hesse, 1938; *phaeopteralis* Hesse, 1938; *poecilopterum* Loew, 1860; *pterostictum* Hesse, 1938; *tinctipenne* Hesse, 1963.

Genus *Mallophthiria* Edwards

FIGURES 341, 522, 532

Mallophthiria Edwards, Dipt. Patagonia and South Chile, pt. 5, p. 169, 1930. Type of genus: *Mallophthiria lanata* Edwards, 1930, by original designation.

Small flies with comparatively short, robust abdomen, with hyaline wings which are virtually identical in venation with *Crocidium* Loew. The face is short and rounded. The males are strongly holoptic and like *Crocidium* Loew there is dense, long, fine pile on head, thorax, and abdomen. They are sharply distinguished by the curious, very much reduced fleshy, stout proboscis with its odd labellum, and by the shorter, different type of antenna. The eye is quite different in shape. Pile of occiput, rather dense, fine, quite long and erect. Ground color black; pile of thorax and abdomen and most of that on face is long, fine, erect, white; some black hair on face and antenna.

Edwards (1930) places this genus within the Phthiriinae probably because of the minute subterminal spine at the apex of the third antennal segment. However, I believe that it is nearer to the genus *Crocidium* Loew and for the present, I leave it next to that genus; only a careful dissection of the genitalia of both sexes and knowledge of the female front can reveal its true relationship.

The face is much shorter than in *Crocidium*; the extremely abundant, long, fine pile on the occiput, face, and gena of *Mallophthiria* is distinctive. While there is some long pile upon these areas in *Crocidium* Loew, it is much more sparse and in that genus the slender, third antennal segment, pointed at the apex, bears a minute microsegment with bristle at tip. *Mallophthiria*

Edwards has a somewhat swollen third segment beyond the immediate base and bears at the apex, a minute, subterminal style or spine inserted dorsally; in this respect it approaches *Phthiria* Meigen. All three genera have broad wings, especially on the basal half, with well-developed axillary lobe and alula, and with generalized venation; all of the cells are broadly open except the anal cell which is closed with a short stalk, or rarely narrowly open in *Crocidium* Loew. In all these genera there are 4 posterior cells, and the discal cell widens very considerably toward its outer end, the intercalary vein long, the anterior crossvein lying near, and in *Mallophthiria* Edwards just before the outer third of the discal cell.

This genus is monotypic and at present only known from a single male from Concepción, Chile.

Length: 4 mm.; wing 3.8 mm.

Head, lateral aspect: The face is very short, its length is a little greater than the thickness of the third antennal segment; the face is, however, quite wide below with an extensive space between the eyes and the oral opening. The oral opening extends back to the posterior eye margin and is twice as long as wide; the sides of the face and the entire lateral and ventral margins and cheeks have a dense fringe of exceptionally fine, long, erect, shining, white pile, changing to blackish immediately beneath the antennae. The occiput is rather thick especially in the middle and below; it gradually narrows toward the vertex, and the medial portion is widely and shallowly concave. The vertical triangle is quite small, a little swollen above the eye margin, equilateral, or short and obtuse, and it extends a little backward behind the eye margin. The front is quite small, extremely small in the male. The eyes are holoptic for four-fifths of the total distance and slightly flattened across the top, no more than in *Crocidium* Loew. The proboscis is short and robust; the labellum forms a more slender but obtuse, short, truncate, slightly curved extension extending upward and lying a short distance beyond the face and composed of 2 divided lappets, one on each side.

The palpi are extremely small, cylindrical, concealed within the oral margin, and composed of 2 segments, the second shorter than the first and with a few fine hairs. The antennae are attached at the upper fifth of the head; they are comparatively short, the first segment is a little longer than the second, the second segment bead-like and as long as wide. The third segment is a little compressed laterally, widest on the basal half, slightly narrowed beyond the middle with a short ventral extension; the apex above this extension bears a minute bristly spine. The third segment has an annulate base; the first segment has rather numerous, long, stiff or bristly dark hairs ventrally and laterally; both first and second segments have some slightly shorter coarse hairs dorsally; second segment with a few setae ventrally. The occiput is quite thick, especially below, gradually sloping to the vertex on the upper half, and it bears exceptionally abundant long, fine, white pile and along

the middle it has a few short, appressed, shining hairs.

Thorax: Densely long, fine, erect, white pilose especially along the anterior half and on the humeri. The pile is still longer and denser on this mesopleuron and there is almost as long, dense pile on the propleuron; pteropleuron and hypopleuron almost or quite apilose; squama with a rather dense, long, fringe of fine pile, opaque and whitish, tufted laterally. The whole of the mesonotum, except perhaps anteriorly, has a few scattered, more or less appressed, short, shining, curled hairs that are continued on the scutellum where there is also considerable long, erect pile. Bristles are absent; scutellum only moderately thick but convex, moderately large and hemicircular.

Legs: The femur is slightly thickened and bears appressed, slightly flattened, shining, white pile; tibia slender, the hind tibia with a dorsal row of very fine, bristly hairs; the hind femur has an anteroventral fringe of long, fine pile, the anterior femur with a more conspicuous posterior fringe of similar pile, over the whole posterior surface. Tarsi have well-developed pulvilli and a short, stiff, bristlelike empodium.

Wings: Very similar to *Crocoidium* Loew, especially *melanopolis* Loew, both of which are here illustrated. The first branch of the fourth vein is slightly arched in *Crocoidium* Loew, nearly straight in *Mallophthiria* Edwards. The second submarginal cell is slightly longer, the anterior branch of the third vein plane except at base. The shape of the discal cell and position of the anterior crossvein and the shape, size, and length of all remaining posterior cells approximately the same in both. Alula and axillary lobe are equally wide. The ambient vein is complete in *Mallophthiria* Edwards, the anal cell closed and stalked; wing hyaline.

Abdomen: Long and conical, or strongly tapered beginning at the base. The base is not quite as wide as the thorax. There are 7 tergites in the male, the seventh is half as long as the sixth, which is in turn a little shorter than the fifth. The lateral portion of the tergites is widely covered with quite long, moderately thick, shining white, erect pile, which continues from the base to the apex, and is somewhat more scanty dorsally. Posterior margins of the tergites with some short, shining, curled hairs.

Material studied: The unique type-species, from which my description and illustration are taken.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical (Chile): *Mallophthiria lanata* Edwards, 1930.

Genus *Desmatomyia* Williston

FIGURES 60, 61, 343, 576, 691, 846, 847, 848

Desmatomyia Williston, Kansas Univ. Quarterly, vol. 3, p. 268, 1895. Type of genus: *Desmatomyia anomala* Williston, 1895, by monotypy.

Small, aberrant, shining black flies with peculiarly plump, thick, slightly decumbent abdomen which at

first sight oddly resemble a blackfly gnat, or simuliid. The ends of the first and second and sixth and seventh abdominal segments are narrowly margined behind with shining yellow. This fly is relatively bare; the pile consists of fine, sparse, more or less erect hairs. No bristles or spines on femora or tibiae.

The proboscis is short and stumplike, the palpus also shortened, with a small oval second segment. Oral recess so shallow as to be almost wanting; it has a narrow fissure in the middle. The antenna is remarkable. The first segment is short, the second still shorter, beadlike; the third segment is elongate, of nearly uniform thickness with the basal segments; near the end it has a second beadlike segment, and beyond there is still another segment which is about 3 times as long as the preceding; both these terminal subdivisions are nearly as thick as the principal part of the third segment.

Wings quite generalized; they are hyaline with short alula and all cells open. There are 2 submarginal cells; the second submarginal cell is long and narrow at base and slightly flared at the apex; its veins end about an equal distance above and below the apex of the wing.

This small fly is known only from the States of Colorado and Arizona.

Length: 5 mm.

Head, lateral aspect: The head laterally is short, oval, and not much higher than long. The occiput, however, is moderately prominent, most extensive where the head joins the thorax and slopes gradually outward to the bottom of the eye, to the lateral margin and to the vertex. The pile of the occiput consists of quite scanty, loosely scattered, moderately long, erect, bristly hairs curved a little outward. The front is slightly convex and raised above the eye margin and bears a few bristles scattered and curved downward along the sides of the front and in front of the ocelli. Face very short from the lateral aspect, its height also much reduced. The pile consists of a few scattered, minute setae.

The eye is large, the postmargin entire but broadly rounded almost as much behind as in front. The proboscis is a curious, short, robust, stout structure thrust forward from the bottom of the eye and scarcely extended farther than the first antennal segment. It has a large, curious, inflated, setate, fleshy labellum. The palpus is equally curious. It is quite large and the first segment thick, a little more than 3 times as long as wide and with some 10 or 12 quite long, slender bristles ventrally and laterally, a few others dorsally and apically. The short, plump second segment is a little wider, bluntly rounded, oval, with 6 or 7 bristles shorter than those of the first segment. Both segments have micro-pubescence. The antennae are attached very near the middle of the head. They are large, robust and long, about $1\frac{1}{3}$ times as long as the head. The large, stout, first segment is barely longer than wide, shining and bare, except for some short setae dorsally and a clump of rather long bristles laterally and ventrally. The second segment is equally wide, much shorter, less than half as long as the first segment, and has a few

setae above and below. The third segment at the base is a little wider than the second segment. It is not extended above the second segment, but is extended below the second segment. This segment is thick, though a little flattened and curved, largely bare, black and shining, and bears at the apex 2 curious microsegments both quite stout and robust. The first is short, shorter than high, the third is about 3 times as long as wide and blunt at the apex. This segment has a somewhat spoon-shaped or cuplike recess situated ventrally and subapically, and bears a spine.

Head, anterior aspect: The head is as wide as the mesonotum. There is a distinct small depression on the medial eye margin opposite the antennae. The ocellar triangle is small and high, the ocelli occupy nearly an equilateral triangle and there are a few erect, bristly setae within this triangle. Middle of the female front with a conspicuous, broad, concave depression running vertically. The oral opening is extraordinarily shallow, almost nonexistent. There is a vertical, curved depression running down each side of what corresponds to the gena. This genal area is very wide and in fact the whole interocular space in front is very wide. The sides of the oral cavity are delimited by a curious, moderately wide, but concave ridge extending from the base of each palpus about halfway up the head toward the antennae. All the intervening area is quite shallow. Tentorial fissures fused. Pile seems to consist of a few microscopic setae.

Thorax: The thorax is comparatively high and compact, the coxae compacted below. Nevertheless, the mesonotum is not high and humped, it is only moderately elevated and is more abruptly convex behind than in front. It is largely bare and has only a few, fine, scattered, erect hairs on the disc. A few longer ones on the notopleuron, a slightly more dense tuft on the humerus and none along the anterior margin. The scutellum has a few scattered, erect, not very long hairs. Mesopleuron has a tuft of a few scattered hairs on the upper half. Pteropleuron and metapleuron bare. I find no pile at all on even the upper and posterior hypopleuron. There are a few setae on the lower edge of the spiracle. Sternopleuron with pollen only. There is a thin, knifelike narrow plate separating the blackish, shining mesonotum from the blackish pleuron below. This plate is pale yellow. Squama large with a rather short fringe. The haltere is quite large with unusually long club, the upper half curved inward longitudinally.

Legs: The legs are short and quite stout, especially the femora, though they are not swollen toward the base. All the femora are shining with numerous strongly appressed, coarse setae of no great length. The tibiae are similarly covered with coarse, subappressed setae and on the hind tibia there are 1 or 2 slightly longer, erect setae dorsally. Tarsi stout and short. Pulvilli long and wide, rounded apically, claws stout, a little curved at the apex.

Wings: There are 2 submarginal cells, the second submarginal cell is rather long and narrow, widening close

to the apex. It arises gradually at the base, and is shaped much as in *Phthiria* Meigen. There are 4 posterior cells which are all long and open maximally. The anterior crossvein enters the discal cell just before the middle. The third vein bends downward at its origin below the second vein. The discal cell is relatively short and wide, strongly angulate below where it is widest. The anterior intercalary vein is one-third as long as the medial crossvein. Axillary lobe broad. Alula 2 or 3 times as long as wide. Ambient vein complete. There is no basal comb.

Abdomen: The abdomen is stout and plump, at the base a little wider than the mesonotum, widest at the end of the third segment and the remainder of the abdomen triangular with the segments rapidly narrowing. There are 7 tergites and a like number of sternites visible. The abdomen is polished, shining, brownish black with the posterior margins of the tergites and the pleuron between tergites and sternites all light yellow. The posterior yellow border of the first and second and the sixth and seventh tergites is much more extensive than that of the others. In some lights there is a faint yellowish white bloom. The pile is very scanty and extraordinarily fine, erect, and not very long. Female terminalia surrounded by strong, curled, flattened hairs turned inward.

The male terminalia from dorsal and lateral aspect, epandrium removed, show dististyli strongly attenuate and strongly divergent. The base of the epiphallus is funnel-shaped. Basistylus bowl-shaped, the epandrium large and long, narrowing apically.

Material available for study: Two females of the type-species. These flies have a curious tendency to become greasy. Dr. Painter gave me one female.

Immature stages: Unknown.

Ecology and behavior of adults: These little flies can be swept up at times from fields of flowers upon open mesa. A single female was collected by Marguerite Hull in middle Arizona in 1959.

Distribution: Nearctic: *Desmatomyia anomala* Wiliston, 1895; *binotata* Painter, 1968.

Genus *Apatomyza* Wiedemann

FIGURES 97b, 349, 544

Apatomyza Wiedemann, Nova Dipteriorum genera, p. 11, 1820.
Type of genus: *Apatomyza punctipennis* Wiedemann, 1820.
by monotypy.

Flies of medium size which superficially resemble a large culicid or empidid. The abdomen is tapered, gradually narrowing, densely short appressed pilose and only half as long as a wing. At the base it is as wide as the anterior mesonotum. The thorax is the most prominent part of the fly, distinctly widest across the base of the wings and the mesonotum rather strongly humped. The comparatively small head is only as wide as the anterior part of the mesonotum; it is rather small, decumbent, with a conspicuous cervix so

that there is quite a gap between the occiput and the mesonotum. The proboscis is slender, thrust directly forward and not longer than the antenna. The antennae are peculiar for the very long first antennal segments which lie adjacent to one another. The third segments are rather strongly and conspicuously divergent. From the dorsal aspect the eyes are strongly cut away yet rounded on the posteromedial corners, leaving a very extensively exposed occiput, with conspicuous mound-like ocellarium. The mesonotum is covered with short semirecumbent pile. The wings are subhyaline with dense, brownish-yellow villi and an iridescent reflection and narrow, diffused, brownish infuscation at the cross-veins, base of the third and fourth posterior cells and of the second submarginal cell. The costal and subcostal cells are light yellowish brown. The ambient vein is complete but weak. The alula is narrow.

This fly is known only from the Cape of Good Hope, and the unique type was collected in October 1817.

Length: 6 mm. exclusive of head. The semidecumbent head including antennae and proboscis measures just over 2 mm., and of about equal length. Wing is 7.5 mm. from apex to extreme base.

Head, lateral aspect: The head is nearly globular but anteroventrally it has an almost rectangular appearance, due to a rather flattened front, a rectangular protrusion of the face beneath the antennae, and the quite plane border from the bottom of the eye to the angle of the face. The occiput from the lateral aspect is quite circularly rounded, not prominent immediately behind the high conspicuous ocellar tubercle, but becoming strongly and almost equally protuberant on the upper half and lower half. The whole posterior profile is quite rounded, and the occiput is also rather extensive at the bottom of the eye, continuing forward as the gena which is almost as wide as the palpus. The upper part of the occiput is blackish and ground color, obscured by yellowish-brown pollen or micropubescence. There are some scattered, pale, brassy, shining, slightly flattened hairs, both above and below, all of which are quite appressed. In addition there are numerous though not dense, long, erect, stiff, brassy, yellow hairs extending almost straight outward. They are shortest on the lower third occiput and much more scanty. The ground color of the occiput toward the middle and also on the ventral fourth or more and upon all of the gena and face, and the lowest half of the front, is rather light brownish yellow. The posterior eye margin is strongly rounded. The facets are large and coarse and tend to appear to be quadrate rather than hexagonal. The upper facets are not larger.

The face is extended forward beneath the antennae, and there is a shallow diagonal fissurelike crease meeting in the midline a short distance below the antennae and then extending a short distance downward and obliquely to the eye margin opposite the proboscis. The face is densely covered with appressed brownish-yellow pubescence and a few short, shining, suberect, yellowish hairs. The front from the lateral profile is visible

across the middle but there are two rather prominent bullae, one on each side at the base of and surrounding the side of the antennae which is visible laterally to some extent. Dorsally the tufted pile that lies on the front and eye margin just opposite the anterior ocellar is conspicuous and consists of a broad, wide clump of more or less appressed, somewhat flattened, golden hairs or scalelike hairs, curled forward and over. The ocellar tubercle is quite conspicuous and high, and the ocelli are large. Between the ocelli is a patch of stiff, black, bristly hairs curved forward and of no great length. There are also a few small, reddish-golden ones.

The proboscis is comparatively stout for the size of the fly but it is nowhere swollen. It is slightly wider apically than on the basal third and distinctly pointed above and below near the apex. On the ventral margin there are a few distinct slender, bristly hairs. They are shorter and more numerous on the basal half, larger and more conspicuous apically, and the entire proboscis has several rows of minute, dense, shining, brownish-golden, erect, micropubescence. The palpus is long, and conspicuous and rather stout. The basal segment is longer than the remaining segment. There appear to be two apical segments. One is short and clavate and round, separated from the middle segment by a distinct oblique suture with even a crease and the base of the middle segment narrowed and attached angularly to the long basal segment. The antennae are attached a little above the middle of the head, and are comparatively stout and elongate. The first segment is at least 5 or more times as long as the second, cylindrical, and of about uniform thickness, and at least as thick as the apical part of the proboscis. It is pale, brownish yellow with a few, fine, scanty, appressed hairs dorsally and a few appressed, more stiff or stouter bristly golden hairs, also flat-appressed ventrally and laterally, placed near the apex. The second segment is not quite as long as wide, brownish, with a very few appressed setae. The third segment is slightly widened to the middle and then rather strongly narrowing to the apex. It is more strongly narrowed below. It is brownish yellow, with minute, erect, shining, yellow micropubescence. At the apex there are two distinct and one very minute micro-segments, the latter bearing a short spine.

Head, anterior aspect: The head is not quite as wide as the anterior part of the mesonotum. The face below the antennae is distinct, and there is an oblique crease-like fissure circling immediately below the antennae, and extending downward to the eye margin opposite the proboscis base. This narrowing extension laterally below the face in front, probably constitutes the gena, and the crease is equivalent to the tentorial fissure. In any case it leaves a shining, rather bare, quite narrow, cuplike margin along the oragenal cup. From the anterior aspect this oral opening is quite large, wide, extending backward a little beyond the bottom of the eye and moderately deep on each side of the proboscis. The front is quite as wide as the face, the upper part slightly wider. Face or front not quite but almost one-third the

total width of the head; this is the male. There is a distinct, horizontal, narrow, linear, brownish band or stripe across the middle of the eye which was probably more distinct in fresh living specimens; eye was probably greenish in life. The antennae are adjacent to one another and continue adjacent throughout the length. The ocellar tubercle is indeed quite large, wide, conspicuous and high. The anterior ocellus is large. The oral opening is large, wide, relatively deep, only slightly narrowed anteriorly. The gena bears minute micropubescence.

Head, dorsal aspect: Viewed from above the semi-decumbent head, the elongate antennae are extended horizontally forward, the vertex is slightly wider than the front. There is a distinct, medial concavity or depression over the whole front from the base of the antennae nearly up to the ocellus. The posteromedial corners of the eye are conspicuously cut away so that the occiput is unusually prominent, bulging backward and sloping strongly downward as well, and with fairly numerous, erect bristly hairs. The attachment to the thorax is small, the prothorax is prominent, also with bristly, subappressed back-turned hairs.

Thorax: The thorax is higher than long, rather strongly humped both anteriorly and posteriorly. The prothorax is prominent from all angles and bears a dorsolateral tuft of appressed, backwardly turned, stiff, bristly, golden hairs. It is dark brown laterally on each side, rather light brownish yellow in the middle; this middle portion is covered with extraordinarily minute pollenlike micropubescence. In consequence the head is well removed from the thorax compared to many bombyliids. The mesonotum is black, except laterally and on the humerus, postalar callosity, and the scutellum, all of which are entirely yellowish brown. The yellow color laterally is more extensive in front of the wing and on the notopleuron. The transverse suture is subcircular, tending to curve a little backward near the top of the mesonotum. In the midline there is a rather wide, posteriorly furcate, opaque black stripe. Another stripe not split posteriorly on either side begins about half way between the humerus and the suture, and there is a diffuse, oval, obscurely blackish spot on each side above the base of the wing, well separated from the latter and more or less confluent with the lateral black stripe. The intervening stripe on each side of the midline has a blue or greenish-black appearance. It may be due to the color of the overlying pollen.

All of the mesonotum is opaque or subopaque and there is a fine, light yellow pollen or micropubescence overlying the brownish-yellow areas. The humerus is paler, and has a tuft of stiff, almost bristly pile over most of the surface. The dorsal pile of the mesonotum is rather abundant, quite flat-appressed, brassy yellow, and slightly flattened or subscaliform. On the notopleuron there are numerous comparatively long back-turned, slender, golden bristles, and a few also behind the suture. Postalar callosity with a few, short, bristly hairs. Scutellum semicircular, brownish yellow, bearing

dense micropubescence, and some short appressed golden hairs; on the margin there are 5 or 6 pairs of distinctly longer slender bristles; all of its pile and bristles brownish yellow to golden. The mesopleuron has much quite appressed, stiff, bristly, somewhat flattened, golden, subscaliform hairs. There are special tufts turned backward on the posterior margin, backward from the anterior corner and dorsally along the upper margin. Pteropleuron, metapleuron, metanotum, and hypopleuron all bare, except for yellow or brassy micropubescence. There are a few appressed bristly hairs on the upper part of the sternopleuron. The whole pleuron is yellowish brown, except that most of the mesopleuron is dark brown to blackish; the anterior half of the sternopleuron is brown. Halteres conspicuous, the knob elongate oval with a lateral fissure. Squama with a fine fringe of moderately long hairs. I do not find a plumula, but there is a small flangelike extension from the side of the scutellum near its base, to the metanotum beneath the inner corner of the squama.

Legs: The anterior and middle femora are distinctly though slightly swollen, gradually through the middle. All of the legs are light brownish yellow becoming a little paler on the tibia and very densely covered with flat-appressed setae, some of it scalelike, and especially scalelike on the lateral surface of the hind femur where it forms conspicuous, matted, longer, scalelike hairs. There are 3, short, small, blackish bristles on the posterior surface of the middle femur, 1 before the middle and 2 near the apex. On the hind femur, more in evidence when viewed ventrally, there are 4 rows of oblique, sharp, rather short, comparatively small, distinct black bristles. All of them are confined to the outer two-fifths. There are 7 subventrally on the lateral surface, 6 ventrolateral; 4 others are ventral and lie near the apex; 6 others are ventromedial in position. The tarsi are slender, pale brownish yellow, with rather dense, minute, appressed, brassy-yellow bristly hairs; on the anterior pair 5 short black bristles are placed posteroventrally, 5 others placed postdorsally, and anteriorly there is 1 at the apex. Middle tibia similar with 8 bristles in the middle posteriorly, 8 posteriorly along the ventral border, and 7 or 8 posteriorly along the dorsal border; also, there are 6 along the middle of the anterior surface. Hind femur with similar bristles and the same number of rows, and generally with 1 or 2 more bristles in each row. There is also an extra row which is anteroventral. The pulvilli are well developed, the tarsi about as long as the tibia; middle tarsus with a rather long, conspicuous, basally stout, pale-colored bristle ventrally, not present on the other tibia; claws slender.

Wings: Comparatively large, and at least twice as long as the abdomen, with a uniform pale, brownish-yellow tint due chiefly to dense villi of the same color. There are no bare areas. The wing is very slightly broader beyond the end of the anal cell and is broadly rounded apically, not pointed. There are 2 submarginal

cells, the second trumpet-shaped, and only a little wider apically, the anterior branch of the third vein arises in a gentle arch with a thickening near its base, and the anterior branch is exactly at the wing apex. The posterior branch ends near the plane of the hind margin. The first and second posterior cells are widely opened, equally wide, and only a little less wide than the apex of the second submarginal cell. Second submarginal cell at apex and the third submarginal cell of about equal width. There are 4 posterior cells; the anal cell is closed with a short stalk, the axillary lobe is a trifle wider than the anal cell, the alula present but narrow and slightly curved. The ambient vein is complete and the posterior fringe is long, fine, and dense. Setae along the costal margin extremely fine and oblique. The posterior crossvein is long, more than half as long as the anterior crossvein. The discal cell ends rectangularly. There is a distinct vein thickening, also, in the middle of both anterior and posterior crossveins, the discal crossvein and again in the lower vein which begins at the middle of the discal cell. The first branch of the radius is thickened and strengthened especially on the outer part. The anterior crossvein enters the discal cell near or just before the outer third of this cell.

Abdomen: The abdomen is distinctly tapered or narrowed posteriorly. There are 8 tergites visible dorsally and laterally, and the ninth forms a short, hoodlike extension over the genitalia; this appears to constitute the epandrium. The abdomen is only half as long as the wing and brownish yellow throughout, except obscurely along the lateral margins, which are blackish. The epandrium is also darker. The pile is flat-appressed, coarse, pale brassy yellow, curved or curled, and bristly. There are a few fine, moderately long, erect hairs along the side margin. The genitalia are terminal and exposed both laterally and apically. The basistylus is large, boatlike, extruded beyond the eighth sternite and distinctly curved upward. The dististyli are a little flattened, curved and diverging outward. From the lateral aspect these structures of the genitalia extend upward as a doubled, clawlike structure.

Material available for study: I have had the good fortune to study the unique type of Wiedemann, the only known specimen, through the courtesy of Dr. Lyneborg of the Copenhagen Museum and of Dr. L. V. Knutsen of the National Museum of Natural History.

Immature stages: Unknown.

Ecology and behavior of adults: Unknown and not on record.

Distribution: Ethiopian: *Apatomyza punctipennis* Wiedemann, 1820.

Genus *Adelogenys* Hesse

FIGURES 223, 301, 564, 568, 1003, 1004, 1005

Adelogenys Hesse, Ann. South African Mus., vol. 34, p. 811, 1938. Type of genus: *Adelogenys cuticoides* Hesse, 1938, by original designation.

Hesse (1938), p. 813, key to 3 species.

Small, rather bare, sparsely pilose flies which appear larger because of the length; they are black flies with often much red or yellow on parts of them. The abdomen is attenuate as well as lengthened which gives the flies a somewhat therevid-like appearance; the bare head is strongly subglobular, the wings hyaline and large in proportion to the body of the fly. The thorax is rather strongly humped and somewhat compressed laterally. The ocelli sit upon a relatively large tubercle and the eyes of the male are separated by at least the tubercle width. The antenna is slender and elongate; the first segment is less than 3 times as long as wide, much shorter than in *Apatomyza* Wiedemann and very much more slender than in that genus; the second segment is minute and beadlike. The third segment is lanceolate, widest near the base, elongate and tapering to the apex which bears 2 short microsegments, the last one having a style.

The wings are very long in proportion to size of the insect; all cells open maximally except the anal cell which is closed with a short stalk. The venation is quite generalized and simple; the intercalary vein is reduced, the anterior crossvein lies at the middle of the discal cell; alula narrow.

These flies are related to *Crocoidium* Loew, differing in the following particulars. The wings are often spotted. The inner margins of the female eye distinctly diverge anteriorly. The genae are always present, the alula and axillary lobe broader, the thorax less humped and the occiput is more or less concave, in contrast to *Adelogenys* Hesse. From *Apatomyza* Wiedemann it differs in the much shorter first antennal segment which is much thinner, but thick and stout in *Apatomyza* Wiedemann.

These three genera stand off to themselves in this subfamily; it may be noted, however, that the small size of *Adelogenys* Hesse, together with the strong hump on the thorax, may indicate a somewhat distant relationship with *Mythicomyia* Melander with its reduced venation and still more extraordinary hump, and minute size.

This genus is restricted to South Africa.

Length: 2.5 to 7.3 mm.; wing 3 to 8 mm., often longer than the insect.

Head, lateral aspect: The head is almost globular due to the strong, posteriorly developed occiput, which is, however, gradually rounded and sloped outward and not cup-shaped. The face is short but produced forward a little beneath the antennae making a right angle with the large, plane, oragenal cup. The face is without pile except for 1 or 2 minute scattered hairs near the oral margin. There is an extremely microscopic, sparse, scattered pubescence along the outer margin of the oragenal cup, which in profile is almost level with the rounded eye margin against which it abuts; the gena is wanting due to the compression of the eye against the oragenal cup. In profile the occiput is almost as rounded as the anterior half of the head, the pile while still scanty is a little more abundant on the upper half

of the occiput where it consists of scattered, metallic, flat-appressed scales. Upper half of the front is similar, with smaller, scattered, appressed scales. The posterior margin of the eye is entire, is very broadly rounded, or rather it is rounded and peaked backward in the middle and less strongly rounded on the upper and lower halves. The proboscis varies from short to long, being in some species at least $1\frac{1}{2}$ times as long as the head and in any case the proboscis is stout and large for the size of the head and the labellum large and conspicuous. The palpus is elongate and slender and conspicuously projecting as in *Crocidium* Loew. It consists of 2 segments, the first one quite elongate and slender, the terminal segment much shorter and broadly ovate or clavate apically with minute hairs. The front is flattened and bare, except on the upper half, which has flat-appressed pile.

The antennae are attached at the middle of the head, relatively slender, almost as long as the head. The first segment is twice as long as wide, 2 to 3 times as long as the short second segment. It is nearly bare, a little widened apically and has a few minute hairs at the apex. Second segment likewise with a more dense micropubesence apically. Third segment is longer than the first two combined, a very little wider than the first segment, and near the outer third it rapidly narrows; the blunt apex bears 2 distinct, narrow microsegments, the first one short, the last one tipped with a bristle. Again, in some species the third segment may be attenuate on more than the apical half, or the segment may be slightly humped, even somewhat spindle-shaped and viewed from above in some species, the basal half is narrowed and the outer half widened toward the middle.

Head, anterior aspect: The head is of approximately the same width as the thorax. The eyes are narrowly separated in the male by slightly less than the width of the ocellar triangle and in females separated by twice the width of the male vertex. The ocellar tubercle is rather large, quite prominent and elevated. The ocelli occupy an equilateral triangle. The oral opening is quite large, shallow throughout, even behind, and it is gradually and slightly widened posteriorly. The genae are virtually obliterated and represented by a scarcely visible line along the eye margin. From a vertical aspect the occiput is completely flat behind and below the ocelli so that there is no trace of groove.

Thorax: The thorax is convex viewed from the side, posteriorly and especially anteriorly and somewhat compressed laterally. The pleuron appears to be comparatively high, due, perhaps, to the somewhat compacted and shortened thorax; this shortening is even more in evidence on the lower half of the thorax with both anterior and middle coxae large and elongate. The pile of the thorax consists of scattered, flat-appressed, metallic scales on the dorsum, some longer, similar hairs on the notopleuron above the wing, and a few shorter scalelike hairs plastered flat and directed backward over the upper half of the mesopleuron. At the upper border

of the mesopleuron a few of these are longer and directed upward. Humerus with 2 or 3 long, brassy hairs. Scutellum subtriangular with rounded apex and elevated above the abdomen due to the prominent metanotum over which it hangs; its pile is somewhat similar to that of the mesonotal dorsum. Postalar callosity shelflike and even concave dorsally. Haltere unusually large, the apical club clavate, rounded, elongate, swollen, and nearly half the length of the haltere. Pteropleuron and hypopleuron bare. Metapleuron with a few minute hairs appressed below the haltere.

Legs: The legs are unusually elongate and slender, especially the hind pair. There are no spines on the femur and the femoral pile consists of moderately abundant, flat-appressed, inconspicuous scales or scale-form hairs. Spicules are reduced and inconspicuous, absent on the anterior tibiae, or at least microscopic and appressed. The hind tibia has 7 or 8 widely spaced, small posterodorsal spicules. Hind tarsi quite elongate, longer than the tibia. Pulvilli long in both sexes and the claws well developed but slender and only shallowly curved.

Wings: The wings are unusually large, elongate, hyaline, villose with 2 submarginal cells and 4 posterior cells, all open maximally. The intercalary vein is short, rectangular; the anterior crossvein is at the middle of the discal cell, the anal cell is closed with a short stalk and the stalk may be obliterated. Axillary lobe large, but alula greatly reduced or almost absent. The venation is quite similar to *Crocidium* Loew. The second submarginal cell is shaped more as in *Mallophthiria* Edwards, but in that genus, among other things, the alula is quite well developed. In *Adelogenys* Hesse the ambient vein is weak. In all three of these genera the anterior branch of the third vein is characteristically straight and not sinuous and bent as in many Bombyliinae, and the second submarginal cell is not wide at the base.

Abdomen: The abdomen is elongate but quite strongly tapered from the base to the apex, relatively bare with wide, yellowish, posterior margins on the tergites and the middle of the first three often widely yellowish, with or without central brownish spots. The scanty pile consists mostly of a fringe of long, flat-appressed, brassy hairs along the posterior margin of the tergites plastered back upon succeeding segments and with some shorter hairs in between. The hypopygium of the male is enlarged, clublike and conspicuous, the large dististyli are ventral and fully exposed below. I find 9 tergites in the male, the last one forming a well-developed shield on the genitalia. Female terminalia small with a fringe of fine, long, posteriorly directed hairs from the last tergite.

I quote Dr. Hesse as follows:

Hypopygium of known male very much like those of *Crocidium*; the basal parts similarly shaped; beaked apical joints flattened dorso-ventrally and bifid apically, the outer apical part being produced spine-like, forming a bifid process with beak; aedeagus as in *Crocidium* and without a ventral process;

lateral ramus on each side, joining each basal part to aedeagal part, also broadish and fange-like as in *Crocidium*; lateral struts slightly more rod-like than shown in figure.

Material available for study: Several individuals most kindly furnished for dissection and study by Dr. A. J. Hesse; as I have only seen the type-species, I have supplemented my description with notes from Dr. Hesse.

Immature stages: Unknown.

Ecology and behavior of adults: Hesse states that these flies resemble mosquitos when resting upon the flowers of *Mesembryanthemum* sp.

Distribution: Ethiopian: *Adelogenys braunsii* Hesse, 1938; *culicoides* Hesse, 1938; *namaquensis* Hesse, 1938.

Genus *Semiramis* Becker

FIGURE 325, 535

Semiramis Becker, Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 17, p. 486, 1913a. Type of genus: *Semiramis punctipennis* Becker, 1913, by original designation.

Semiramis Becker contains small flies which appear to be closely related to *Crocidium* Loew. I have not seen these flies, but it is apparent from Becker's figure of the wing and profile figure of the head that only slight differences of wing shape and slight differences of cell shape separate it from *Crocidium* Loew. Not only this, but both genera have punctiform spots about the crossveins and vein intersections. Becker, the author of this genus, compared it to *Geron* Meigen, from which it is both obviously and abundantly distinct. Since Becker did not mention *Crocidium* Loew, it can only be assumed that it did not occur to him to compare them.

The wing is a little more pointed apically, and in this respect a little more like *Geron* Meigen; but the cells are remarkably like *Crocidium* Loew; the anterior crossvein is a little closer to the middle of the discal cell, but this, of course, varies some in most genera. The second submarginal cell is longer and narrower in *Semiramis* Becker than in *Crocidium* Loew, and the stalk of the anal cell is longer, the first branch of the medius is perhaps slightly more arched. I have reproduced Becker's figures.

The single known species is from Persia.

Length: 4 mm.; wing 3.5 mm.

I have not seen this fly and I quote Becker's description:

Habitus as in the case of *Geron* Meigen. Thorax and abdomen not broad, with only delicate and short sparse hairs, without bristles. Antennae close together; first and third segments elongated, narrow, the latter with only a short central terminal bristle, without a visible style. Eyes in the female widely separated, in the male without indentation (concavity) on the posterior margin. Lower part of the face short, projecting forward, slightly cone-shaped. Proboscis protruding by a head's length in front of the edge of the mouth, projecting forward horizontally with very long, thread-like, 2-segmented palpus. The posterior margins of the abdominal segments are distin-

guished by special coloration. The legs are fairly long, without bristles. Venation as in the case of *Phthiria*, with 2 submarginal cells and 4 open posterior cells; the first is widely opened, on the wing edge almost twice as wide as in the middle; anal cell closed and stalked. The junction of the veins are margined with brown.

Type in the museum of St. Petersburg.

Material available for study: None.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic: *Semiramis punctipennis* Becker, 1913.

Genus *Tamerlania* Paramonov

Tamerlania Paramonov, Trav. Mus. Zool. Kieff, p. 203, 1931a. Type of genus: *Tamerlania grisea* Paramonov, 1931, by original designation.

I have not seen *Tamerlania* Paramonov and I quote the original description, taken by Engel from Paramonov:

Closely related to the genus *Semiramis* Becker, but the venation is somewhat different; the anal cell is opened fairly widely at the margin; the anterior crossvein stands somewhat before or at the middle of the discal cell, and not behind the middle as is the case of *Semiramis* Becker. The branches of the third longitudinal vein are relatively short, only placed a very little closer to the base of the wing than the apex of the second longitudinal vein (very significant in the case of *Semiramis*); the lower branch is straight, the upper one bent in a definite S-form and arises at an almost right angle (in *Semiramis* the two branches are almost straight, and the upper one arises at a very acute angle); the first posterior cell becomes gradually broader over its entire length (without narrowing in the middle). Remaining venation almost the same as with *Semiramis*.

The body is weakly haired and almost without bristles. Upon the thorax, in front of the base of the wings, there is a distinct bristle. The tibiae are short, but distinctly bristled. Abdomen uniformly black. Pulvilli distinct; (in *Semiramis*?). The structure of the antenna differs somewhat perhaps from that of the species of *Semiramis*, but the description of *Semiramis* in Becker is less detailed (Paramonov).

Paramonov describes the type-species in the following words:

The whole body is black, dusted heavily with gray. The face is very slightly protruding in profile; between the mouth and the cheeks there is a groove. Cheeks and chin have sparse but long and whitish hairs. The mouth opening is quadrangular with right angles. The front (frons) is very broad, the vertex of the head takes up considerably more than one-third of the width of the head; toward the bottom the front gradually becomes wider. The ocellar tubercle takes up considerably less than one-third of the width of the vertex; it is covered with extremely short whitish hairs. The front has a distinct transverse groove somewhat above the base of the antennae; below this trough the surface is completely hairless; above it the front is somewhat long, but bears scant, erect, mixed black and yellow hairs; the first segment is almost one and one-half times longer than the second; the third segment is bare, without an easily discernible style or microsegment; it is somewhat blunted at the end, almost one and one-half times longer than the two first segments together; it is somewhat thickened in profile at the basal part, becoming more narrow toward the apex. The indentation on the posterior margin of the eyes is completely missing.

The occiput has sparse, but fairly long whitish hairs; it is fairly flat, without a longitudinal groove or a strongly emphasized central concavity. The proboscis is almost one and a half times longer than the head. The antennae are very long, reaching almost two-thirds the length of the proboscis, somewhat shaped at the apex. Mesonotum with two darker longitudinal lines in the middle, with sparse black and white erect hairs, no scales or bristles, except there is a distinct bristle in front of the base of the wings. The pleura are almost bare, only the mesopleura have sparse but fairly long whitish hairs. The halteres are yellow, the head as long as the stalk. The legs are black, without bristles (on the hind femur there are only long bright colored hairs). The tibiae, however, are short black bristled, the under side of the tarsi likewise. The legs without scales. Wings clouded quite milkily, most blackly bordered along

the veins. The costa surrounds the whole edge of the wing. The abdomen on the tergites and sternites is sparsely whitish haired. According to its whole habitus, this fly resembles a species of *Conophorus* Meigen (Paramonov).

Three females (not well preserved examples) Tshangyr, N. W. Buchara, 27 April 1930 (I. Zimin. leg.).

Length: 3-4 mm; wing length: 3-4 mm.

Material available for study: None.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic: *Tamerlania grisea* Paramonov, 1931.

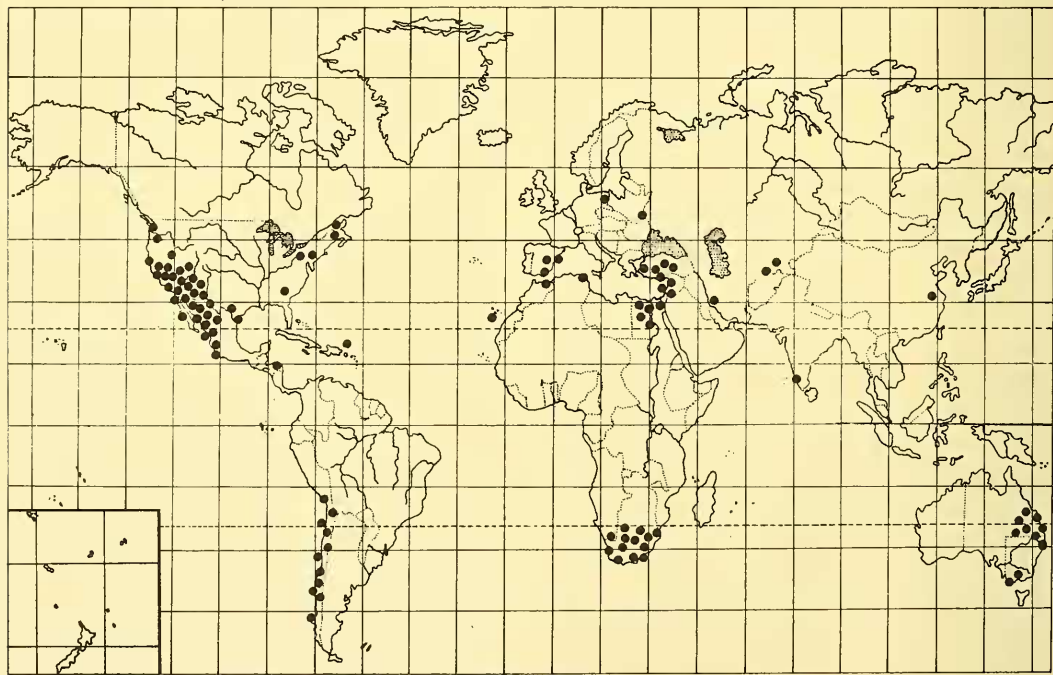
Subfamily Phthiriinae Becker, 1912

This group has in the past served as a dumping ground for a number of quite disparate elements. Fortunately Hesse (1938) recognizing this, transferred such elements as *Adelogenys* Hesse and *Apatomyza* Wiedemann and *Crocidium* Loew back to the Bombyliinae; for them I erect the tribe Crocidini; Hesse also removed the *Geron* Meigen group to a well-marked new subfamily; the genera like *Apolysis* Loew and *Oligodranes* Loew appear to me to show a much greater affinity to the genus *Usia* Latreille, than to *Phthiria* Meigen, though I admit there is some general similarity in the antennae; nevertheless, the *Phthiria*-type antennae has arisen independently among other bee flies, even in the Bombyliinae. Of course, it would be possible to unite the Usiinae and the Phthiriinae, and there is some justification for this.

In this subfamily as here constituted the only world-wide representative is *Phthiria* Meigen, which appears to be present on all continents; favoring arid lands, it is abundantly represented in the southwestern United States. In the known species the larvae feed within the egg pods of locusts.

The flies of this subfamily may be characterized by the slightly humped thorax, the 4 posterior cells and 2-branched third vein. While the pile and pubescence is generally sparse and scattered and rather short, there are exceptions in such as the almost woolly *Acreotrichus* Macquart from Australia. Most species are either light in color or have much pale color in the form of vittae or paired spots, and there are interesting sex differences. Thus in some Central American *Phthiria* Meigen the males are almost or quite solid black in contrast to much

Phthiriinae



TEXT-FIGURE 24.—Pattern of the approximate world distribution of the subfamily Phthiriinae.

lighter females, and I am indebted to Rex Painter for calling my attention to this. Generally, much of the body is bare. The abdomen may be short, plump, compact, barely tapered or in Egyptian species much lengthened and tapered. There is a distinct and characteristic frontal depression before the antenna. Eyes are not infrequently red or green. Male genitalia are large, terminal, conspicuous. All these flies are relatively small.

I recognize four subgenera under *Phthiria*: *Poecilognathus* Jaennicke, distinguished by the conspicuous vein appendices; *Pygocona*, new subgenus, from the Australian area, distinguished by the peculiar conical hypopygium; *Agenosia*, new subgenus, distinguished by the completely bare genofacial area, and the more extended face which is not rounded and turned in-

ward, also, the more extensive frontal area; and *Neacreotrichus* Cockerell, subgenus, new status.

In the Phthiriinae the male terminalia are large, terminal in position, instead of reflexed downward. They are therefore conspicuous and many of the parts and processes can be inspected without dissection. This is very much in contrast to the subfamily Bombyliinae, in which the genitalia are only rarely enlarged and terminal, as for example in *Acrophthalmyda* Bigot. In the Phthiriinae there are often conspicuous, elongate, accessory prongs or lobes that we here call claspers. This is suggestive of the situation in Gerontinae, but radically different, because in the Gerontinae we have the entire basistylus undivided and all the processes arising as lobelike extensions. All of the processes and the dististylus arise as lobelike processes rather than as separate movable segments.

KEY TO THE GENERA AND SUBGENERA OF THE PHTHIRIINAE

1. First and second antennal segments of nearly equal length and each approximately as long as wide, and with approximately parallel sides. Epandrium, short, mammiform. Upper lateral face and lateral gena with or without pile. 3. First antennal segment clearly longer than wide and longer than the second segment; sometimes 2 or more times as long as wide. Third antennal segment angularly widened near the middle, with a dorsal tuft of several bristles or bristly hairs placed at the hump. 2
2. Face densely covered with pile of medium length. Bristly hairs on antennal segment 3 or 4 in number and not extraordinarily long. Anterior branch of third vein arising gently. Epipygium formed into a long, V-shaped, gaping, dorsal cone. *Phthiria* (*Pygocona*, new subgenus)
Upper lateral face and genal area inflated and densely very long, erect pilose. Anterior branch of third vein arising as a rectangular crossvein with long, backward spur. Dorsal

- angle of third antennal segment conspicuous, with 7 or 8 conspicuous, long bristles, the longer bristles twisted and bent. Second antennal segment also longer than wide. Whole insect densely covered with very long, dense, erect, fine black hair much as in *Bombylius* Linné. Epandrium short and obtuse. *Acrotrichus* Macquart
3. Angular veins and stumps of veins present in the discal cell; anterior branch of third vein usually rectangular with stump vein. *Phthiria* (*Poecilognathus*) Jaennicke
Discal cell without angulated veins and stumps. Anterior branch of third vein always arising gently. Upper genofacial area typically with abundant long hair (if completely bare, *Agenosia*, new subgenus). 4
 4. Third antennal segment with conspicuous long, dorsal bristles. *Phthiria* (*Neacreotrichus*) Cockerell
Third antennal segment with at most minute bristles, hairs, or none. *Phthiria* Meigen, *sensu stricto*

Genus *Phthiria* Meigen

FIGURES 99, 100, 215, 308, 566, 570, 849, 850, 851

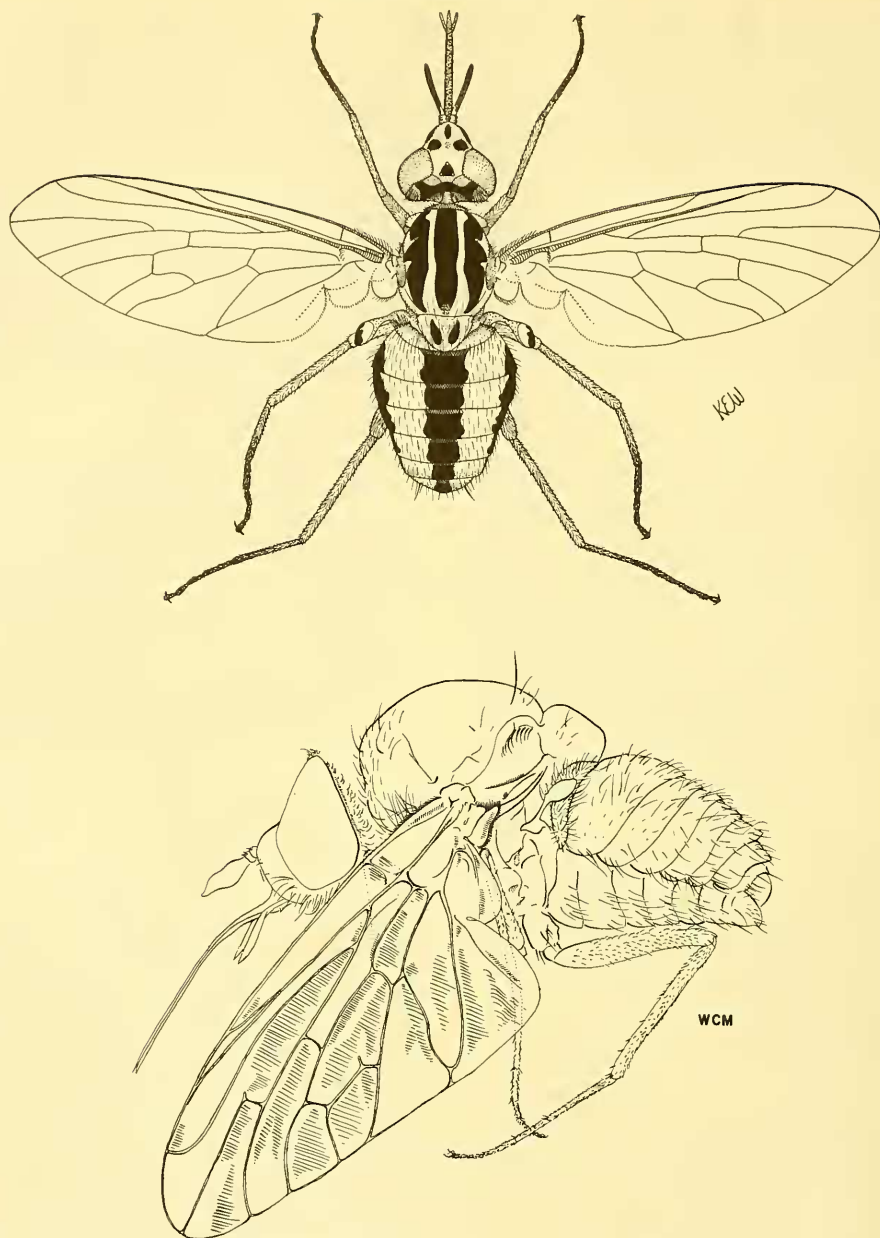
- Phthiria* Meigen, Mag. Insektenkunde, vol. 2, p. 268, 1803. Type of genus: *Bombylius pulicaria* Mikan, 1796, by monotypy.
Cyclorhynchus Macquart, Diptères exotiques, vol. 2, p. 114, 1840. Type of genus: *Cyclorhynchus testaceus* Macquart, 1840, by monotypy. Preoccupied Sund., Aves, 1835.
Cyclorhynchus Bezzi, p. 3, 1924, emendation.
Phthiria Rondani, Arch. Zool. Anat. Fisiol., vol. 3, p. 65 (sep.), 1863, lapsus.
Poecilognathus Jaennicke, vol. 6, p. 350, 1867a. Type of subgenus: *Poecilognathus thlipsomyzoides* Jaennicke, 1867, by monotypy.
Pygocona, new subgenus. Type of subgenus: *Pygocona flavicincta*, new species.
Agenosia, new subgenus. Type of subgenus: *Agenosia vittata*, new species.
Neacreotrichus Cockerell, 1917, subgenus, new status; Proc. U.S. Nat. Mus., vol. 52, p. 377. Type of subgenus: *Acrotrichus atratus* Coquillett, 1904.

- Coquillett (1894), pp. 102-103, key to 10 Nearctic species.
Williston (1901), pp. 288-289, key to 9 Mexican species.
Coquillett (1904b), p. 172-177, key to 12 Nearctic species.
Séguy (1926), p. 234, key to 8 species from France.
Hardy (1933), p. 415, key to 4 Australian species.
Austen (1937), pp. 63-64, key to 8 Palaearctic species.

- Engel (1933), pp. 140-142, key to 27 Palaearctic species.
Hesse (1938), pp. 825-831, key to 8 male, 6 female species from South Africa.
Eflatoun (1945), pp. 107-108, key to 4 Egyptian species.
Painter (1962), pp. 28-29, key to 12 Nearctic species.

Compact, rather small flies ranging in size from about 1.5 millimeters to 5 or more times this size. Some Egyptian species have elongate, tapered abdomens 3 times as long as wide. They generally have short, scanty pile but a few have considerable amounts of longer, fine, erect pile. The coloration is commonly pale with or without dark vittae or spots upon face, front, thorax, and abdomen, but some species are entirely black and others have a very fine pale pollen over the thorax. Painter has called my attention to the marked sexual color dimorphism in some species.

In addition to a long, slightly arched proboscis, the genus is especially characterized by the form of the antenna; the third segment is elongate with the apex hollowed out, liplike above, and jutting from the concave pitlike apex is a minute spine or sensory rod. Also in males the eye is distinctly depressed above, a depression that extends to the front of the female and leaves it quite flattened. The face and front are prominently



TEXT-FIGURE 25.—*Phthiria* species: habitus and lateral aspect.

extended. Wings broad and often quite broad basally. The anterior branch of the third vein and the medial crossvein often have backward spur veins.

This genus is worldwide in extent with rather more species known at this time from the southeastern United States.

Length: About 1.5 mm. to 8 mm., excluding proboscis; wing, 2 to 7 mm.

Head, lateral aspect: The head is sometimes globular and sometimes more or less trapezoidal in shape with the very long front sloping, flattened, or even concave. The occiput varies from short, though moderately and equally extensive above and below, broadly shallowly concave centrally, and this seems to be typical of the genus although there are certainly other species in which the occiput is more prominent and the head subglobular. The occipital pile ranges from scanty, short, stiff, erect, fine, bristly hairs with the eye margin bare to others in which there is rather dense, coarse, bristly pile over almost the entire occiput, the pile below becoming longer and more shaggy. The front in males may be either short, swollen and convex with a complete transverse band of coarse, bristly pile extending all the way around the sides of the antennae and down the sides of the face, or the front may be longer, very little swollen but depressed with a triangular patch of rather dense, appressed, bristly pile reaching from the junction of the eye nearly to the antennae. The females are characteristic in having the front wide and very strongly depressed across the middle with transverse foveal crease, and the pile similar in character to the male. The eye is comparatively large, triangular on the upper half and divided in males into an area of larger facets above and smaller facets upon the lower third of the eye. The upper facets are often greatly enlarged. The posterior margin of the eye is entire.

The face is often rather extensive laterally with the short oragenal cup extending to the base of the antennae, sometimes vertically plane and in other species strongly and convexly retreating below the antennae. The oragenal cup does not always reach the base of the antennae. Sides of face either bare and shining, or with considerable long, coarse, bristly or scaliform pile directed forward. The proboscis is always quite long and slender, more attenuate apically, $1\frac{1}{2}$ to 3 times as long as the head and with the labellum quite slender. It is projected straight forward, sometimes a little curled downward. The palpus is extraordinarily slender and long in some species, in others it is lanceolate, shorter and decidedly more broadened before the apex.

The antenna is attached just above the middle of the head, sometimes more nearly at the upper third. It is comparatively elongate, slender, the third segment flattened. All three segments are of nearly uniform width, although the third segment may be a little wider and is sometimes angularly swollen dorsally to a moderate extent in the middle of the segment. This genus is characteristic in the form of the third antennal segment which at the apex bears a dorsal, liplike process, another

below the apex, which may be shorter or even longer, leaving the intermediate portion of the apex concave and having a short, conspicuous spine. Third segment either pollinose only or sometimes with several short, stout, oblique bristles in the middle on the dorsal surface. The first segment is a little longer than wide, slightly narrower at the base with strong, long, bristly setae above and a few shorter setae below. Second segment about as long as wide and sometimes shorter, either nearly as long as the first segment, or in other species only half as long, and likewise with a few setae dorsally and at the apex. The third segment varies from 2 to $2\frac{1}{2}$ times as long as the first two segments together.

Head, anterior aspect: The head is ventrally comparatively plane, or sometimes with the suboccipital area a little swollen below. The genofacial area is very wide below becoming in the male slightly convergent toward the antennae, or even with the sides parallel as far as the antennae. The eyes are holoptic for an extensive distance in the male and are depressed where the eyes touch, in addition to a slight overgrowth of the eye on each side. The whole upper side of the eye tends to be flattened. Ocellar tubercle small forming an equilateral triangle, the ocelli resting on the eye margin and the tubercle a little swollen and bearing several fine, long, bristly hairs. Front of female widely separated, slightly convergent toward the vertex and the vertex 3 times the width of the posterior ocelli measured from their outer edges. The antennae are narrowly separated; the first segments touch because they are widened apically. The oragenal cup is rather small, shallow, and short oval, the inner wall is quite wide and slightly sloping inward. Both the lateral face and the gena are quite wide and extensive, with either loose or comparatively dense pile continuing down the side, long and erect. Tentorial fissure absent.

Thorax: The thorax is short and compact, the mesonotum rather high, moderately humped and about equally convex anteriorly and posteriorly. The mesonotal pile varies from scanty and erect or suberect in some species to comparatively dense, rather long, and erect but never hiding the ground color in others. However, some species appear to be either naturally almost bare of pile on mesonotum and abdomen or they become naturally heavily denuded in emergence or when swept up in the net. I have before me a very large series of one very polished black and yellow species in which only an occasional scattered hair can be seen on the mesonotum on any one of the many specimens and in which the abdominal pile is also scanty. The mesonotum may be with or without a fine, quite microscopic, scaliform pollen. The humerus is prominent with a deep 3-cornered recess behind. It seems to always bear long pile, and there is coarse bristly pile on the notopleuron; a few fine hairs on the wide and much flattened posterior callosity, especially on its rear margin. The scutellum is quite large, in many species strongly inflated and convex posteriorly and bears fine, erect pile similar in length and abundance to that found on the

mesonotum. If the mesonotum is largely bare, so is the scutellum. The same relationship holds to the mesopleuron and the upper sternopleuron. The pteropleuron, metonotum, the hypopleuron, and the whole of the metapleuron are without pile. Alary portion of the squama large with a scanty fringe. Halteres large with elongate knob and apically widened stalk. Pleuron with or without pollen.

Legs: The legs are moderately long, the femora a little stout, the anterior 4 femora slightly widened toward the base. The hind femur generally slightly widened in the middle. Pile of the femora moderately abundant, obliquely appressed and setate, bristles absent. Tibiae and tarsi a little lengthened and slender. Anterior tibia without bristles or contrasting spicules; the pile consists of appressed setae; other tibiae similarly pilose but in addition they show several rows of oblique, short, stout, spicules. The middle tibia may have as many as 7 or 8 anteroventrally and as many as 15 or 20 dorsally. Hind tibia similar. Claws slender, strongly bent at the apex, the pulvilli long and widely spatulate.

Wings: The wings are hyaline or with spots on the crossveins and wing furcations and sometimes the apices of veins. Characteristically the wing is exceptionally broad at the base. The axillary lobe and the alula are wide. There are 2 submarginal cells and 4 posterior cells, all of them widely open. The anal cell is closed and stalked, the anterior crossvein enters the discal cell always beyond the middle of the discal cell and sometimes at the outer third. The species of *Phthiria* Meigen fall into 2 groups depending on the form and shape of the second submarginal cell and the character of the first section of the anterior branch of the third vein. This first section of the anterior branch of the third vein may be plane and rectangular and simulate a crossvein, with a strong backward spur. In such species there is generally a backward spur at the bend in the lower vein of the discal cell. Painter and Painter (1962) allocate these species to the subgenus *Poecilognathus* Jaenicke. Other species of *Phthiria* Meigen, sensu stricto, have the base of the second submarginal cell arising in a gently rounded fashion, and the lower vein of the discal cell likewise is rounded without a spur. The alula ends at the anal cell.

Abdomen: The abdomen is short and compact and sometimes very short especially in the females, where several tergites are tucked under and recessed below the others. Viewed from above the abdomen is often obtusely conical but in Egyptian species elongate conical, gradually tapered, the sides plane, the whole abdomen 2 or 3 times as long as the basal width. The pile of the abdomen is generally similar to that of the thorax, being very scanty or almost absent on the more bare species, which have a few fine, short, scattered, appressed hairs, and in more pilose species the pile is much more abundant, generally more or less appressed dorsally but forming a conspicuous, erect fringe laterally. In *Phthiria floralis* Coquillett the pile is conspicu-

ous, very fine, long, and erect over the entire abdomen. The female terminalia consist of 2 triangular plates apposed together from each side; from their junction below there are 3 or 4 long, curved, appressed bristles. Male terminalia quite prominent, though not very long, dorsal in position, with the hooks turned downward. The last sternite forms a shelf below with a lateral lobe on each side, the aedeagus lying between.

Since Dr. A. J. Hesse was able to base his conclusions upon a greater number of species, I quote his remarks upon the male hypopygium:

Hypopygium of males with the inner apical part of basal parts in neck region usually prominent or produced into a process, which is broad from side, provided at apex towards the outer side and more dorsally with a crest of shortish spines, with the dorsum of basal parts often provided with long, bristly hairs: beaked apical joints usually slightly curved, hollowed out below, with comparatively few and sparse, or without any, hairs above, but sometimes with a few, usually two, longer, stouter and more spine-like, bristly hairs nearer apex on inner side; aedeagus usually straight or curved upwards apically, without a ventral process, joined on to basal parts on each side by a broadish, flange-like ramus or merely by a strap-like ramus which is under the lateral struts, the aedeagus often produced basally below middle part into a conspicuous process on each side; lateral struts directed outwards and upwards in most of the species.

The male terminalia from dorsal aspect, epandrium removed, show long, slender, apical upturned dististyli which at the apex are apt to bear several very long spikelike spines. In addition, on each side of the epiphallus and in some cases also dorsal medially above the epiphallus, there are apt to be long, accessory, slender, lobelike structures, which in this work we call claspers. The ramus forms a continuous girdle below the base of the aedeagus. In the lateral aspect the basistylus is large, but short oval, the epandrium is triangular with a posterior lobe in the middle, and the basal apodeme quite large and long, with a prominent additional aedeagal apodeme besides the usual lateral apodeme.

Material studied: A large series of several species from the southwestern United States collected by the author and wife, together with several fine pairs exemplifying sexual dimorphism sent to me by Dr. Painter.

Immature stages: The larvae are predators on grasshopper eggs. See discussion in life histories.

Ecology and behavior of adults: These flies are strongly attracted to flowers, especially composites; the author and his wife swept up several species in considerable numbers in the Southwestern States in the fall of 1965. We found one species spread over a hundred-mile area of highway and adjacent fields congregating on sunflower heads in immense numbers. Some of these heads contained as many as 25 individuals, which were greedily at work feeding.

Distribution: Nearctic: *Phthiria aldrichi* (Johnson), 1903 (subg. *Poecilognathus*); *americana* (Coquillett), 1805 (as *Acreotrichus*); *amplipella* (Coquillett), 1904 (subg. *Poecilognathus*); *badia* (Coquillett), 1904 (subg.

Poecilognathus); *bicolor* (Coquillett), 1904 (subg. *Poecilognathus*); *borealis* (Johnson), 1910 (subg. *Poecilognathus*); *cingulata* Loew, 1846; *consors* Osten Sacken, 1887; *coquilletti* (Johnson), 1902 (subg. *Poecilognathus*); *cyaniceps* (Johnson), 1903 (subg. *Poecilognathus*); *diversa* Coquillett, 1894; *egerminans* Loew, 1872; *flaveola* (Coquillett), 1904 (subg. *Poecilognathus*); *floralis* Coquillett, 1894; *humilis* Osten Sacken, 1877; *inornata* (Coquillett), 1904 (subg. *Poecilognathus*); *loewi* Painter, 1965 [= *notata* (Loew), 1863 (subg. *Poecilognathus*)]; *maculipennis* (Cole), 1923 (as *Acrotrichus*); *marginata* (Coquillett), 1904 (subg. *Poecilognathus*); *melanoscuta* Coquillett, 1904; *nubeculosa* (Coquillett), 1904 (subg. *Poecilognathus*); *picturata* Coquillett, 1904; *psi* (Cresson), 1919 (subg. *Poecilognathus*); *punctipennis* (Walker), 1849 (subg. *Poecilognathus*); *scolopax* (Osten Sacken), 1877 (subg. *Poecilognathus*); *similis* Coquillett, 1894; *sulphurea* (Loew), 1863 (subg. *Poecilognathus*); *unimaculata* (Coquillett), 1904 (subg. *Poecilognathus*); *vittiventris* (Coquillett), 1904 (subg. *Poecilognathus*).

Neotropical: *Phthiria albida* Wiedemann, 1821; *alterans* Williston, 1901; *atratus* (Coquillett), 1904 (as *Acrotrichus*; subg. *Neacrotrichus*); *austrandina* Edwards, 1937; *aztec* Painter, 1962; *barbata* Rondani, 1863 [= *barbata* Philippi, 1865, = *vulgaris* Philippi, 1865]; *cana* Philippi, 1865; *chilena* Rondani, 1863; *dolorosa* Williston, 1901 [= *sororia* Williston, 1901]; *exilis* Philippi, 1865; *fasciventris* Twinn, 1928; *fulvida* Coquillett, 1904 (subg. *Poecilognathus*); *lurida* Walker, 1857; *mixteca* Painter, 1962; *olmeca* Painter, 1962; *philippiana* Rondani, 1863; *picta* Philippi, 1865; *pirioni* Edwards, 1937; *pulchella* Williston, 1901; *testacea* Macquart, 1840; *thlipsomyzoides* (Jaenicke), 1867 (as subgenus *Poecilognathus*); *tolteca* Painter, 1962; *tristis* Bigot, 1892.

Palaearectic: *Phthiria albogilva* Séguin, 1941; *atrieops* Loew, 1873; *bicolor* Bezzi, 1925; *cancecens* Loew, 1846 [= *convergens* Loew, 1846, = *pulicaria* Zetterstedt, 1842, = *zimmermanni* Nowicki, 1867, female]; *conspicua* Loew, 1846; *gaedii* Wiedemann in Meigen, 1820 [= *maculata* Wiedemann, 1820, = *punctata* Meigen, 1838]; *incisa* Becker, 1915; *inconspicua* Becker, 1912; *lactipennis* Strobl, 1909; *minuta* (Fabricius), 1805 (as *Volucella*) [= *fulva* Meigen, 1804, = *maura* Wiedemann in Meigen, 1820, = *zimmermanni* Nowicki, 1867, male]; *pulchripes* Austen, 1937; *pulicaria* Mikán, 1796 [= *campestris* Fallen, 1815, = *gibbosa* Walker, 1851, not Olivier, 1789, = *nigra* Meigen, 1804, = *pygmaea* (Fabricius), 1805 (as *Volucella*)], *pulicaria* major, Strobl, 1909; *quadrinotata* Loew, 1873; *rhomphaes* Séguin, 1963; *salmayensis* Efflatow, 1945; *scutellaris* Wiedemann in Meigen, 1820; *simonyi*, Becker, 1908; *subnitens* Loew, 1846 [= *rustica* Loew, 1846]; *tricolor* Bezzi, 1925; *umbripennis* Loew, 1846 [= *notata* Bigot, 1862]; *unicolor* Bezzi, 1925; *vagans* Loew, 1846, *vagans pallescens* Engel, 1933; *variegata* Austen, 1937; *varipes* Austen, 1937; *virgata* Austen, 1937; *xanthaspis* Bezzi, 1925.

Ethiopian: *Phthiria capensis* Wiedemann, 1828; *cognata* Hesse, 1938; *erocogramma* Hesse, 1938; *fallax* Hesse, 1938; *flavigenualis* Hesse, 1938; *laeta* Bezzi, 1921, *laeta xerophiles* Hesse, 1938; *lanigera* Bezzi, 1921; *nigribarba* Hesse, 1938; *pilrostris* Hesse, 1938; *pubescens* Bezzi, 1922; *pulla* Bezzi, 1922; *simmondsi* Hesse, 1938; *tinctellipennis* Hesse, 1938.

Oriental: *Phthiria gracilis* Walker, 1852.

Australian: *Phthiria albocapitis* Roberts, 1929; *flava* Hardy, 1933; *hilaris* Walker, 1852; *lineifera* Walker, 1857; *nigra* Hardy, 1933; *pallipes* Bigot, 1892.

Patria Ignota: *Phthiria cingulata* Loew, 1846; *hypoleuca* Wiedemann, 1828.

The following new species may be added to this list: Nearctic: *Phthiria* (*Agenosia*) *vittata*, new species.

Australian: *Phthiria* (*Pygocona*) *flavicincta*, new species.

Genus *Acrotrichus* Macquart

FIGURES 98, 315, 534, 536

Acrotrichus Macquart, Diptères Exotiques, suppl. 4, p. 121, 1849. Type of genus: *Acrotrichus gibbicornis* Macquart, 1849.

Comparatively small flies which superficially resemble a species of *Sparnopolius* Loew in general shape. The exceptional, long, erect pile of the thorax and still longer, erect, fine pile of the abdomen, spreading outward along the lateral margins and upward dorsally, is of somewhat looser character, and the pile of the face is also very long, erect, and abundant.

They will be quickly recognized by the long, stiff hairs arising from the angulate dorsal margin of the third antennal segment and from the *Phthiria*-like venation in which the anterior branch of the third vein arises rectangularly as a crossvein from which a long spur vein proceeds backward. The face is long pilose in both males and females, in contrast to *Phthiria* Meigen in which only the male face has pile.

These flies are restricted to Australia.

Length: 6 to 8 mm.

Head, lateral aspect: The head is almost triangular at the base because of the remarkable flattened eyes that are depressed along the midline and because of the shortening of the occiput dorsally, a form more or less characteristic of flies in the Phthiriinae. Below, the occiput becomes more extensive from the lateral aspect, but slopes rapidly inward toward the foramen. The pile of the occiput is remarkable for its length. There is a dense band of very long, erect, coarse hair covering almost the whole of the posterior occiput from the vertex to the bottom of the occiput, extending on beneath the eye and up along the sides of the gena from below. In addition and somewhat set apart from the more central band of pile there is a thin, loose fringe of even longer hairs in several irregular rows with attachment close to the eye margin and a short distance behind the eye margin. These hairs are as long as the

eye itself and as long as the elongate third antennal segment. The small ocellar triangle is equilateral in shape, the ocelli rest on the eye margin; it has a tuft of very long hairs in a vertical row, some extend up, others extend forward almost to the antenna.

The front constitutes about one-third of the distance from base of antenna to the posterior eye margin. It bears a conspicuous, appressed, matlike tuft of rather long, coarse, pale yellow pile on each side of the medial line divergent outwardly and reaching to the base of the antenna, and directed obliquely away from the front. The face is bulging and rounded on each side, in length nearly as much as the first antennal segment. It bears rather dense clumps of extraordinarily coarse pile, dark reddish brown laterally, changing to slightly shorter, finer more matted, dense, central tufts of pale yellow pile. There is so much pile on the upper and middle part of the face that the ground color is completely obscured. However, laterally the face has gray pollen on the surface. This long extensive pile continues upward and reaches slightly above the antenna and leaves the nonpileous part of the front dark brown pollinose posteriorly and yellowish pollinose anteriorly. This excessively long pile of the face continues equally densely down the sides of the exceptionally wide gena to merge with the pile at the bottom of the head, the only point where the pile is less dense.

The proboscis and labellum are slender and elongate, $1\frac{1}{2}$ times as long as the head. The long, sticklike, almost filiform palpus is half as long as the proboscis and extends beyond the long pile of the face. It bears a few stiff hairs apically. The antennae are attached a little above the middle of the head. They are elongate with the first two segments relatively stout. The first segment is cylindrical, slightly curved from lateral view, and from 4 to 5 times as long as wide. It bears dense, long, erect pile dorsally, somewhat shorter pile laterally, and some long hairs ventrally. The second segment is longer than wide, distinctly widened apically, at least twice as long as its basal width, and bears a remarkably long, rather dense tuft of stiff, almost bristly hair dorsally. There is similar hair ventrally that is not quite as long and not quite as much. The third antennal segment is as long as the first two together and strongly flattened, rather strongly widened dorsally at the middle, and bears at the middle a tuft of 4 long and 3 or 4 very long, bent, curved bristly hairs. They arise laterally just below the high point of the third segment. Apex of the third segment with a short, dorsal, blackish spur and concavity in which there is a yellowish spine, and the ventral lobe that extends conspicuously outward is much thicker and 4 or 5 times as long as the dorsal lobe, and represents the true apex of the third segment.

Head, anterior aspect: Much wider than the thorax. Oval from the anterior aspect because of a shortening and flattening of the head on the lower half. The upper half of the head forms, if it were continued uniformly, half of a circle. Upper eye facets enlarged, but no

demarcation between the facets at the bottom of the eye. The eye of the male is conspicuously and tightly holoptic for two-thirds the distance from antenna to occiput. The antennae are quite narrowly separated at the base. The oral cup is obscured by pile, but is rather large, quite short, oval, and deep. Its inner edge is sharp. The genofacial space is strongly widened and expanded, leaving the extensive cheek occupying almost one-third the total width.

Thorax: Subquadrate, only a little wider across the anterior edge of the postalar callosities. The mesonotum is gently convex, a little more so anteriorly. The head is a little drooping. The pile of the mesonotum is opaque black, shining on the scutellum, and densely covered with exceptionally long, nearly or quite erect, coarse, bristly, pale, shining, yellowish-white pile. There is no anterior collar, and pile similar to the mesonotum occurs on the scutellum. There are no bristles. Pleuron with conspicuous pile, extraordinarily so over the whole mesopleuron, radiating out as long, dense tufts. Pteropleuron, anterior hypopleuron, and the metapleuron bare. However, there is a conspicuous tuft of long, erect pile on the posterior hypopleuron above the hind coxa. And there appears to be a knoblike process arising well below the wing attachment between the wing and the base of the haltere bearing radiating pile. This structure is presumably the outer edge of the squama, and the pile is apparently the pile of the plumula extending on medialward. It may also represent a shelflike extension of the squama.

Legs: The legs are rather long and well developed; hind femur stout, but not swollen, a little flattened. The anterior and middle femora bear dense fringes of long pile ventrally, anteroventrally, and posteroventrally. Dorsally on each side they have some appressed, slightly flattened, bristly hairs. Hind femur with a moderate amount of long pile ventrally, especially on the basal half, becoming shorter distally, with considerable appressed, flattened golden pile distally along the lateral margin, and also dorsally and medially. Surface of this femur transversely microrugose. The long tibia have appressed setae on the anterior pair, small, oblique bristles on the others, situated in 4 rows. Posterior tibia with 7 short, stout bristles ventrolaterally, the same number anterodorsally, and about 15 dorsomedially, fewer ventromedially. Claws long, sharp, rounded, but most rectangularly bent apically, and with the pulvilli large and long.

Wings: Nearly hyaline, broad basally, distinctly pointed apically. Almost all the veins are nearly straight with at most slight curvatures, the cubital vein more strongly curved than any. The second vein arises before the end of the second basal cell and is quite straight. Third vein straight to the beginning of the second submarginal cell, which arises by a rectangular, straight, crossvein-like vein and has an equally straight backward spur, which is longer than the basal part of the anterior branch of the third vein. This basal spur presumably represents the remnant of the atrophied

third branch of the radius (second branch of second vein). The anterior crossvein enters the discal cell at the outer fourth. The first posterior cell is open maximally, the second posterior cell is widened apically, the third is slightly narrowed, the discal cell is elongate and angular below. Medial crossvein long, nearly straight but slightly wavy, upper anterior intercalary vein straight and longer than the anterior crossvein. Anal cell closed with a long stalk, the lower vein straight, axillary lobe large and alula quite large. The ambient vein ends at the anal cell. The costal comb is not developed, but there is a tuft of hair arising below from the extreme base of the wing.

Abdomen: Short oval and as long as the mesonotum if the scutellum is excluded. The abdomen is blunt, obtuse, and plane apically. There are 7 tergites visible from above, the last three of nearly equal length, and narrowing a little posteriorly. The ground color is opaque black. The pile on the central part of the disc is fine, erect, and quite long, but becoming much more dense gradually toward the sides of the abdomen, which are curled over; it presents a very bushy appearance indeed. This lateral pile is as long or longer than the facial pile. The male terminalia are large. The basal parts are large, rather rounded or subcircular, convex

and a little swollen outwardly, covered with moderately long bristly hair, and with the small, attenuate dististyli lying side by side, separated but slightly convergent apically and directed downward. These parts are exposed from the rear aspect and tucked beneath the last tergite. Sternites completely obscured by the long, lateral pile and the curving under of the tergal margins.

Material available for study: Representatives of this genus were found in the collections of the National Museum of Natural History. This well-characterized fly was collected September 9, 1902, near Windsor, New South Wales, by W. W. Froggatt.

Immature stages: Unknown.

Ecology and behavior of adults: Hardy (1922) writes:

... this is the first species of bombyliid to appear in the spring, and it continues on the wing through the summer; it occurs everywhere that wild flowers are abundant, and at times 20 or 30 specimens can be taken with one sweep of the net, and indeed sometimes they are so abundant that they continuously divert one's attention from other insects.

This abundance must be relatively uncommon.

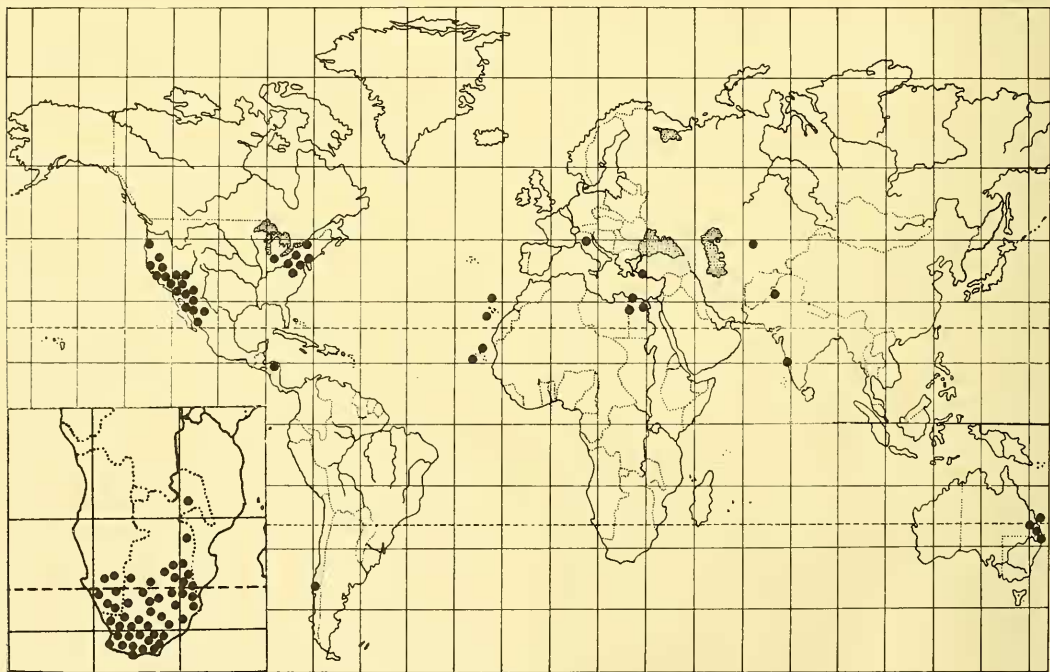
Distribution: Australian: *Acreotrichus fuscicornis* Macquart, 1849; *gibbicornis* Macquart, 1849; *inappendiculatus* Bigot, 1892.

Subfamily Gerontinae Hesse, 1938

This subfamily proposed by Hesse in 1938 appears to be well founded. Although small, it is worldwide or very nearly so. It may be defined by the following 9 characteristics: (1) Flies with never more than 3 posterior cells. (2) In contrast to *Phthiria* Meigen the face below the antenna is extensive. (3) Genal pile, usually present, is stiff, appressed, or curled upward. (4) A discal cell is always present. (5) The first antennal segment is elongate, usually much more than $1\frac{1}{2}$ times as long as the second; it is generally very short in the Phthiriinae. (6) The last sternite of the female is divided, with lappetlike lobes. However, in many species of *Phthiria* Meigen this sternite is deeply concave, with widely separated lobes or prongs. (7) The third antennal segment is elongate, slender, strongly tapered, drawn-out to a fine pointed apex. (8) The wing is broad at base, the anal cell closed and stalked; in this respect they are similar to *Phthiria* Meigen.

Proboscis is long and slender in both, the latter has a quite long slender palpus, the *Geron* Meigen species a short slender palpus. *Geron* Meigen has a more narrow, less extended oragenal cup. The venation of the two groups has features in common. It is possible that in the remote past the Gerontinae arose from the *Phthiria* stem by loss of a posterior cell and a different direction to the antennae; both have the front depressed; or possible from a *Gonarthrus*-like fly. (9) The male genitalia are very complex with numerous prongs and spurs. This is evident in *Geron* Meigen, but even more so in the curious South African *Pseudoamictus* Bigot where the terminalia are conspicuous, larger, and more exposed.

In the Gerontinae the male terminalia are much more complex and radically different from similar structures found in either the Bombyliinae or the Phthiriinae. They especially differ in the structure of the basistylus,



TEXT-FIGURE 26.—Pattern of the approximate world distribution of the species of the subfamily Gerontinae.

which is undivided and not separated into symmetrical halves. Moreover, there are no separate and distinct movable dististyli, this structure being replaced by curious, hornlike lobes or processes from the distal part

of the basistylus. Much of the basistylus is membranous. There may be additional hornlike or spinelike prongs on each side of the epiphallus and aedeagal complex.

KEY TO THE GENERA OF THE GERONTINAE

1. Genae very wide, the oral cavity, including the lateral ridge, only about half the width of total space between the eyes on the lower part of head; oral cavity more shallow. Face below antennae pollinose, without pile; genal pile much more extensive on lower third or more of head, long, abundant, bristly, appressed upward. Male eyes rather widely separated or not in contact, or separated by only the width of anterior ocellus, the front therefore much more extensive. First antennal segment as long as others combined, strongly thickened, especially at base, and with dense, long erect, bristly pile extending over its whole length. Whole fly longer, less wide at base, less tapered posteriorly. Wing more elongate, sometimes wholly reddish brown, anal cell closed in the margin, apical cell narrow, the vein closing the middle posterior cell conspicuously sinuous *Pseudomicetus* Bigot
- Genae never extraordinarily wide, usually linear. Oral cavity very deep. Face below antenna with abundant, long, erect pile. Genal pile scanty, largely limited to bottom of eye, curled upward and shorter. Male eye holoptic for a very short distance, depressed at juncture, the male front very small, the ocellar tubercle small but conspicuous. First antennal segment elongate but shorter than remain-

- ing two segments, more slender, its pile shorter, and distinctly appressed. Wing broad at base, the anal cell stalked or petiolate, wing almost always hyaline; vein closing middle posterior cell only gently curved. Whole fly shorter, more robust at base distinctly tapered posteriorly 2
2. Male and female face beneath the antenna bare or at most with a few hairs. Pile of first antennal segment long, copious, erect. Anteroventral genal pile abundant. Genae as wide as first antennal segment; third antennal segment pointed but quite long *Amictogeron* Hesse
 - Male and female face with abundant, long erect pile beneath the antenna. Pile of first antennal segment, shorter, scantier, distinctly appressed. Anteroventral genal pile scanty. Genae quite linear. Third antennal segment shorter, pointed, more strongly tapered (*Geron* Meigen, and subgenera) 3
 3. Length of last section of fifth branch of radius to the edge of wing about as long as the preceding portion extending to anterior crossvein *Geron* (*Empidigeron*) Painter
 - Length of last section of fifth branch of radius to the edge of wing never more than two-thirds as long as preceding section to the anterior crossvein, and often much less (*Geron* Meigen, sensu stricto) *Geron* Meigen

Genus *Geron* Meigen

FIGURES 104, 105, 309, 523, 543, 754, 755, 859, 860, 861

Geron Meigen, Systematische Beschreibung, vol. 2, p. 223, 1820.
Type of genus: *Bombylius gibbosus* Olivier, 1789, as *Geron gibbosus* Meigen, 1820. Designated by Rondani, 1856. Not *Bombylius hybridus* Meigen, 1804, as given by Bezzi, p. 2, 1924, which is a synonym of *B. gibbosus* Olivier.

Empidigeron Painter, subgenus, Trans. American Ent. Soc., vol. 58, p. 143, 1932a. Type of subgenus: *Geron snowi* Painter, 1932a, by original designation.

Bezzi (1924), pp. 112-113, key to 11 Ethiopian species.
Paramonov (1929), p. 185, key to Palaearctic species.
Painter (1932), pp. 144-146, key to 19 Nearctic species.
Engel (1933), pp. 132-133, key to 5 Palaearctic species.
Hesse (1938), pp. 873-883, key to 23 South African species.
Eflattoun (1945), pp. 136-137, key to 7 species and subspecies from Egypt.

Small to medium-sized black flies with only the tibiae and basitarsi and sometimes the femora yellow or brown. They are readily recognized by the presence of only 3 posterior cells, the basally stout, conically tapered abdomen which is a little compressed laterally, the humpbacked mesonotum, and the characteristic antenna. The elongate third antennal segment is strongly tapered from base to apex so that it ends acutely and much attenuate and tipped by a minute, short spine.

The wings are hyaline; the first submarginal cell is short and the anterior branch of the third vein arises in a steep arch; the anal cell is closed. The vestiture of these flies consists of sometimes dense, sometimes sparse,

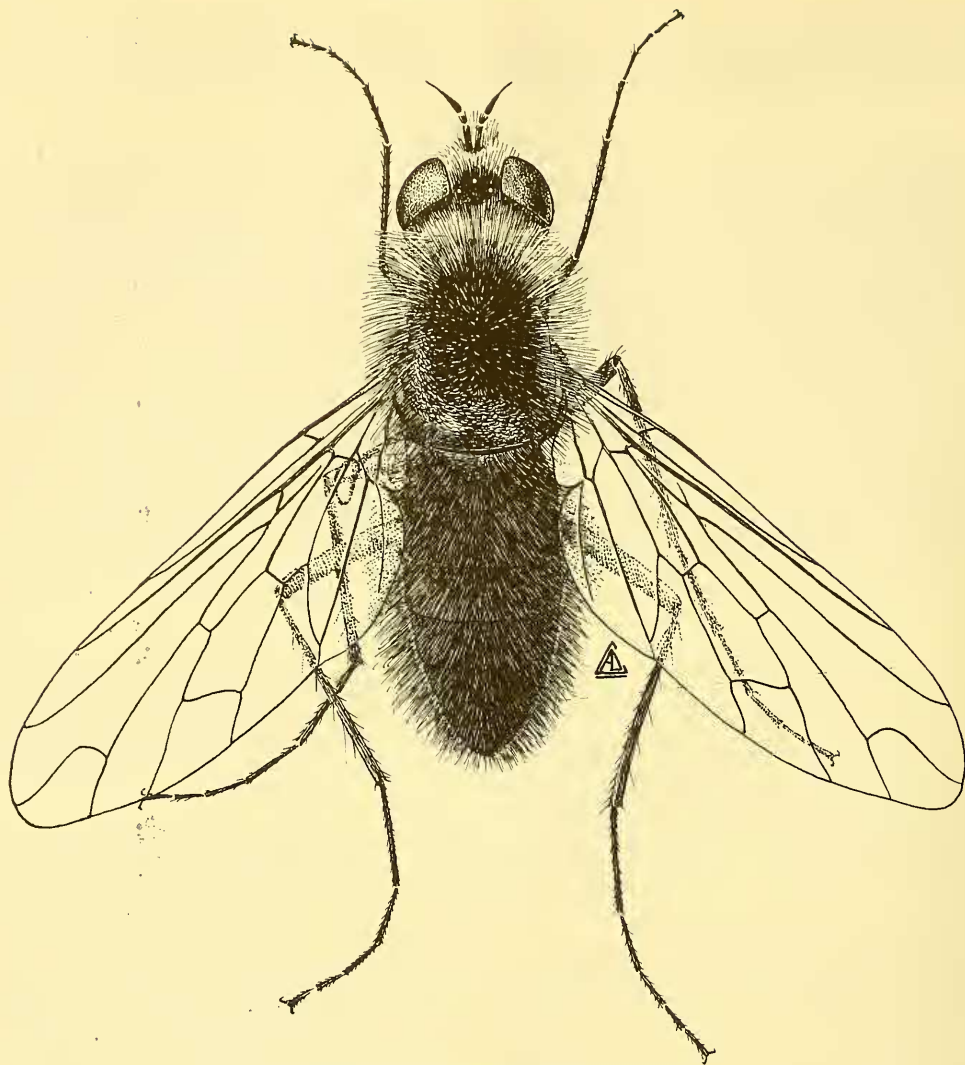
long, fine, erect pile in which there is frequently much, short, glittering, narrowly scaliform and curled or appressed pile on front, mesonotum, and especially the abdomen. Females tend to have more glittering, curled, appressed pile, therefore, the sexes are somewhat dissimilar in appearance. They become very readily denuded.

This genus is distributed through the Palaearctic region on down into Australia; it extends into South Africa, and Chile, and with 22 species in the United States.

Length: 3 to 9 mm. including antenna; wing 2.5 to 8.2 mm.

Geron Meigen, has one subgenus: *Empidigeron* Painter. These flies are characterized by the relative length of the last section of the fifth branch of the radius; this section is relatively long. In *Geron* Meigen in the strict sense, the last section of the fifth branch of the radius is always less than two-thirds the length of the preceding section of that vein as it ends at the anterior crossvein; it is usually much shorter so that the apical cell is relatively short and broad rather than relatively long and narrow as in *Empidigeron* Painter, the flies of which are less numerous and found in the Southwestern United States.

Head, lateral aspect: The head is subglobular, strongly and convexly rounded on the anterior half and with a rather prominent swollen occiput especially in the middle of the head, sloping gradually downward, upward and toward the sides of the eye margin. In the

TEXT-FIGURE 27.—Habitus, *Geron senilis* Fabricius.

males the upper occiput is more shallow, in the females more extensive. The pile of the occiput is long, dense, and bristly with some shorter, flat-appressed, curled, glittering, scaliform pile intermingled and reaching quite to the eye margin. The front is somewhat flattened, generally plane with the eye, and there is characteristically a low, foveal depression transversely across the lower front shortly in front of the antennae. In males the front and the junction of the eye margins

are distinctly sunken with the whole upper occiput flattened and plane from the lateral aspect and the upper half of the eye triangular. The pile of the small male front is pollinose with a few appressed, scaliform hairs in the middle and along the eye margin. The ocellar tubercle is strongly swollen with a tuft of coarse, erect, bristly hairs, and the ocelli rest almost on the eye margin. The pile of the front in the female is pollinose, often dark in the center but silvery on the outside and

with either a band of long, coarse, shining bristles down the middle of the front, curved forward, or with flattened scales laterally and smaller, flat-appressed, curled, scaliform pile in the middle or with the long medial bristles wanting.

The face is quite short in profile; both have broad, appressed scales near the eye margin and some longer, slender, generally silvery bristles directed downward along the sides. The walls of the oragenal cup are short, rimlike, following the convex contour of the eye to the bottom; gena absent. The outer margin of this wall is obliquely steep, yet short, is pollinose, and may possibly be considered genal. The posterior eye margin is plane. The proboscis is quite long and very slender, 2 or 3 times as long as the head, the labellum equally slender, the palpus slender but short, bearing several setae at the apex. The antennae are attached near the upper third of the head, they are slender and elongate, the first segment is 2 to 3 or more times as long as the second segment and has quite abundant, long, fine, oblique bristles or bristly setae. The second segment is cylindrical, of uniform width and usually slightly longer than wide. Third segment a little longer than the first two segments together, very strongly tapered and attenuate to the apex, which bears a distinct apical spine. The basal fifth of the first segment is widest, not quite as wide as the second segment.

Head, anterior aspect: The head is quite circular, the eyes widely holoptic in the male for a distance 4 or 5 times as long as the front but in the female the eyes are widely separated and only slightly convergent dorsally. The vertex is about 3 times as wide as the distance between the posterior ocelli. The antennae are narrowly separated at the base, the oragenal cup is more or less rectangular and quite deep with steeply slanting interior walls. Dorsally it begins a long distance from the antennae, and hence the face beneath the antennae is almost as long as wide. There is no tentorial fissure, and the gena appears to be absent except for a minute trace below.

Thorax: The thorax is compact with the mesonotum strongly humped and convex, a little more so anteriorly. The pile of the mesonotum is scanty, fine, and either erect or suberect, very easily denuded, remnants of pile more apt to be preserved along the anterior margin. In females the pile is generally much more abundant, dense, long and bushy; it is better preserved on the anterior third of the mesonotum posteriorly and on the scutellum; mesonotum always pollinose, and rather feebly shining. The humerus is densely pilose, the notopleuron likewise with at most very slender bristles. The pile of postalar callosity is similarly bristly and the scutellum with dense, fine, long, erect pile, except when denuded. In addition to the erect pile both sexes tend to have a varying amount of brilliant, glittering, gold or silver, short, curled, appressed, scaliform pile. The pleuron is pollinose; whole of the mesopleuron and upper sternopleuron densely, long pilose, the latter also with some shining, appressed scales; pteropleuron,

metanotum, the anterior metapleuron, and the hypopleuron without pile, except there may be a small patch of scales at the bottom of the pteropleuron, and a patch of scales and some long hairs are on the posterior metapleuron. The alary portion of the squama is moderately long with a radial tuft of long hairs at the lateral corners, and sometimes a scanty fringe over the remainder of the border; halteres large, posteriorly elongate.

Legs: The legs are moderately long and slender, including the femora. The femoral pile consists of matted, flat-appressed scales and a fringe of stiff, shaggy pile ventrally on all three pairs. The anterior tibia has only fine, small, appressed, setate pile; spicules absent, except for perhaps 2 or 3 very minute, short, oblique, slender bristles which are scarcely noticeable. On the middle and hind tibia the spiculate bristles are somewhat longer, still quite slender, oblique, and few in numbers, usually about 3 to 5 dorsally, sometimes as many as 10 on the hind tibia in the anterodorsal row, 6 in the anteroventral row and the same number in the posteroventral row; tarsi rather long and quite slender; claws slender, nearly straight, except at the apex where they are curved; pulvilli long.

Wings: The wings are hyaline, and rather broad at the base, though never as much so as in *Phthiria* Meigen. Most of the veins are weak but distinct. There are only 2 submarginal cells, and it should be noted that there are only 3 posterior cells. The anal cell is closed with a long stalk; vein closing the discal cell either nearly straight or slightly sigmoid. The anterior cross-vein enters the discal cell at or just beyond the middle. The second submarginal cell in *Geron* Meigen, *sensu stricto*, is quite short, but in the subgenus *Empidigeron* Painter it is nearly twice as long as wide.

Abdomen: The abdomen is moderately elongate, at the base nearly or quite as wide as the mesonotum and strongly and characteristically tapered and generally compressed laterally, so that viewed laterally it is rather high. It is only about as long as the thorax with the scutellum included, sometimes slightly longer and occasionally shorter. The pile, except in denuded individuals, is very fine, quite long and erect, varying in quantity and with a considerable amount of curled, flattened, scaliform, glittering pile which is silvery or golden in color. Although it varies, females tend to have more of the glittering pile on both abdomen and thorax and either somewhat less or somewhat shorter, erect, shining pile. The female terminalia consist of the short, conical, or triangular eighth tergite, laterally compressed into 2 shorter, apposed flaps posteriorly, the last sternite making a well-separated, shovellike extension below. The male terminalia consist of an elongate pair of apposed or narrowly separated, spike-like or thornlike protuberances, which represent the apices of the basistyli with the more slender, sharper processes of the dististyli lying between; this is the digitate form of the genitalia of Painter (1932); they

also occur in what Painter calls the rosette form. He says that these forms are interchangeable.

Inasmuch as Dr. A. J. Hesse has been able to dissect more species than I have I quote his remarks on the male genitalia:

Hypopygium of male like that of the other *Geroninae*, is more complicated than in any other genus belonging to the *Bombyliidae-Homocophthalmae*. The hypopygium can only be satisfactorily studied in a liquid medium. As in other *Geroninae* the basal parts form a single structure, not being divided into two symmetrical parts by a dorsal suture or impression and what is designated by me as dorsal is more commonly ventral in position in the intact and set insect, the aedeagus and its attendant structures being more constantly dorsal in position. The basal part is usually more membranous than chitinous on each side towards the apex, the membranous part not having hair or only a few bristly hairs. The dorsum sometimes with hairs towards apex and in some cases with a few or a row of distinct hook-like spines on each side. The distinct and freely movable beaked apical joints of other *Homocophthalmae* are entirely absent, being represented simply by scarcely movable lobes, by paired or symmetrical extensions, processes or lobes apically on the basal part. These processes in *Geron* assume various shapes in the different species and are thus of taxonomic value in their separation. They are lobe-like, spine-like, hook-like, or dentate and are represented singly, in duplicate or even in triplicate on each side apically. The aedeagal apparatus is complex, composed of a medium straight, curved or even duplicated aedeagus proper ending basally in a spoon-shaped or ladle-like structure, which has a lateral, flattened or flap-like process on each side, corresponding to the lateral struts of other *Bombyliidae* and a dorsally directed bat or racket-shaped basal strut as in other *Bombyliidae*.

The medial aedeagal structure passes through a central guide which is usually produced into a flattened lobe-like process on each side towards base and apically is often pitchfork-like, produced into a long apically directed, straight or curved, spine-like or sabre-like process or prong on each side of the aedeagus either above or below. These prongs, when present, together with the aedeagus, are lodged in or more to and from in a central or median dorsal guide in the form of a partially chitinous or entirely chitinous trough-like or sheath-like structure, usually thinned out towards base or apex or broadened apically or basally, where it is also joined on to the subsidiary apical processes or lobes of the basal part by means of ligaments or membranes. In some species where the central guide is not produced apically into a prong there is nevertheless present on each side a curved or U-twisted spine. Ventral to the aedeagus the central guide abuts, or is joined, on to the basal part apically on each side by a raised strap-like or arch-like ramus, which is sometimes produced apically into a prominent flattened, lobe-like or even spine-like process.

The male terminalia from dorsal aspect, epandrium removed, show a complex dististylus with several accessory lobes all narrow, mostly curved outward and downward. The ramus is small and makes a transverse bridge above the epiphallus. Laterally the basistylus is large, and high, that is, extensive dorsally. The epandrium is subtriangular.

Material studied: A considerable series of many species from Mississippi and the Southwestern United States.

Innate stages: These flies are parasites of tortricid, pyralid, and psychid moths. See discussion under life histories.

Ecology and behavior of adults: These flies come to flowers but are not restricted to composites, though they more often are found there. I have frequently collected them from the heads of composites and have noted a characteristic habit of bobbing up and down several inches above the flower head before settling upon it. They also hover in sunny spots. Painter (1932) states that some species, including the large species *Geron grandis* Painter, are partial to button bush, *Cephalanthus occidentalis*; he also notes that they may be found at the tips of twigs resting much as some asilids do.

On a research collecting expedition to New Mexico, in September 1967, the author collected 99 individuals of a species of this genus in about 20 minutes on a patch of sticky, yellow-flowered composite, *Haplopappus ciliatus* (Nutt.) DC., no more than 50 yards long by 10 yards wide, near a west Texas highway; many others were left; only a small clump of trees was nearby among open fields. Almost without exception these flies selected unoccupied flower heads upon which to alight. One fly was snatched by a small spider as it alighted. Possibly this marked habit of bobbing up and down upon flower heads before alighting is a precautionary instinctive habit. No less than six species or types of spiders were seen on these flower heads besides reduviids; phymatids were absent.

Distribution: Nearctic: *Geron aequalis* Painter, 1932, subg. *Empidigeron*; *albarius* Painter, 1932; *albipennis* Loew, 1869; *arenicola* Painter, 1932; *argutus* Painter, 1932; *aridus* Painter, 1932, subg. *Empidigeron*; *calvus* Loew, 1863, subg. *Empidigeron* [= *macropterus* Loew, 1869]; *digitarius* Cresson, 1919; *grandis* Painter, 1932; *holosericeus* Walker, 1849 [= *versicolor* Painter, 1932]; *hybus* Coquillett, 1894, subg. *Empidigeron*; *johnsoni* Painter, 1932; *nigripes* Painter, 1932; *niveus* Cresson, 1919; *nudus* Painter, 1932, subg. *Empidigeron*; *pavidus* Painter, 1932; *robustus* Cresson, 1919 (as subsp. of *digitaria*); *snowi* Painter, 1932, subg. *Empidigeron*; *subauratus* Loew, 1863; *trochilus* Coquillett, 1894; *vitripennis* Loew, 1869; *winburni* Painter, 1932.

Neotropical: *Geron albus* Cole, 1923; *albidus* Walker, 1857; *canus* Philippi, 1865; *colei*, nomen nudum; *insularis* (Bigot), 1856 (as *Bombylius*); *litoralis* Painter, 1932; *niveoides* Cole, 1923; *rufipes* Macquart, 1846; *senilis* (Fabricius), 1794 (as *Bombylius*) [= *albipennis* Loew, 1869, = *vitripennis* Loew, 1869]; *trochilides* Williston, 1901; *insularis* Cole.

Palearctic: *Geron coregreus* Frey, 1936; *emiliae* Zaitsev, 1964; *garagniae* Efllatoun, 1945; *gibbosus* Olivier, 1789, *gibbosus erythropus* Bezzi, 1925, *gibbosus halteralis* Wiedemann in Meigen, 1820, *gibbosus subflavofemoratus* Rubio, 1959 [= *capensis* Walker, 1852, = *gibbosus* Meigen, 1820, = *hybridus* (Meigen), 1804, as *Bombylius*], = *olivieri* Macquart, 1840]; *hesperidum* Frey, 1936; *intonsus* Bezzi, 1925 [= *krymensis* Paramonov, 1929]; *longibarbus* Efllatoun, 1945; *longiventris* Efllatoun, 1945; *phallophorus* Bezzi, 1922; *priapeus* Bezzi, 1922.

Ethiopian: *Geron anceps* Hesse, 1938; *australis* Hesse, 1938; *bechuanus* Hesse, 1936; *delicatus* Hesse, 1938; *dichroma* Bigot, 1892; *dissors* Hesse, 1938; *dubiosus* Hesse, 1938; *furcifer* Hesse, 1938; *gariepinus* Hesse, 1938; *luctipennis* Hesse, 1938; *latifrons* Hesse, 1938; *lepidus* Bowden, 1962; *maculifacies* Hesse, 1938; *munroi* Hesse, 1938; *mystacinus* Bezzi, 1924; *nasutus* Bezzi, 1924; *nigerrimus* Hesse, 1938; *nigrifacies* Hesse, 1938; *niveus* Hesse, 1938; *nomadicus* Hesse, 1938, *nomadicus breyeri* Hesse, 1938; *orthoperus* Hesse, 1938; *peringueyi* Hesse, 1938 [= *hybridus* Bezzi, 1921, not Meigen]; *psammobates* Hesse, 1938; *semifuscus* Ségné, 1933; *transvaalensis* Hesse, 1938; *turneri* Hesse, 1938; *parvus* Hesse, 1938.

Oriental: *Geron albescent* Brunetti, 1909; *argenti-frons* Brunetti, 1910.

Australian: *Geron australis* Macquart, 1840; *cothurnatus* Bigot, 1892; *dispar* Macquart, 1849; *hilaris* White, 1917; *nigralis* Roberts, 1929; *simplex* Walker, 1859.

Oceania: *Geron umbripennis* Bezzi, 1926.

Patria Ignota: *Geron ?tenuis* Walker, 1857.

Genus *Amictogeron* Hesse

FIGURES 106, 310, 530, 537, 776

Amictogeron Hesse, Ann. South African Mus., vol. 34, p. 918, 1938. Type of genus: *Amictogeron meromelas* Hesse, 1938, by original designation.

Hesse (1938), pp. 921-929, key to males of 15 species, females of 12 species.

Small flies that resemble *Geron* Meigen and with which it is closely related. It may be distinguished by the absence of pile upon the face and the slender, much longer, much less attenuate third antennal segment; also males bear very long, dense bristly pile all around the surface of the long, basally swollen first antennal segment, much in contrast to the males of *Geron* species known to me. The second submarginal cell is long as in *Geron* Meigen.

These flies have a convex and humped mesonotum as in *Geron* Meigen. The head is subglobular, the male eyes extensively holoptic, whereas this genus has long, upturned oragenal pile, none on face; *Geron* Meigen is the reverse, it has facial pile, none on the oragenal strip. Hesse (1938) gives the following additional differences from *Geron* Meigen species known to him:

First antennal segment longer than in *Geron* Meigen, at least 3 and usually much more than 3 times as long as second segment; antennae more widely separated at base than in *Geron* Meigen, but less widely than in *Pseudoamictus* Bigot; third antennal segment more slender than in *Geron* Meigen, more rod-like and more slender, ending in a scarcely visible terminal microsegment which ends in a minute style or spine; palpi very slender, longer than in *Geron* Meigen; upper and lower veins of second submarginal cell generally nearly parallel; alula narrower and less developed than in *Geron* Meigen.

The apical crossvein of discal cell usually more distinctly sigmoid than in *Geron* Meigen; laterally the tergites below do not overlap the sternites as in many species of *Geron* Meigen;

spicules of tibiae usually more poorly developed than in *Geron* Meigen; erect pile of the body less dense and shorter even in males than *Geron* Meigen; hairs of first antennal segment and of gena, denser, longer, more bushy, and often very conspicuous in contrast to *Geron* Meigen; no flattened, silvery scalelike pile on the head behind the eyes, on gena, or on frons as is so characteristic of *Geron* Meigen.

Hesse also contrasts minor differences between the terminalia of the genera. He notes a pronounced sexual dimorphism in *Amictogeron*; females having more yellowish markings on pleuron and abdomen, paler or more yellowish femora and tibiae, no long bushy hairs on first antennal segments, no basal pronounced knob-like thickening on first antennal segment, shorter and sparser pubescence on the body, and denser scaling. I have quoted these distinctions from Hesse since the three paratypes of the type-species before me are in very bad condition.

Hesse notes that this genus can only be confused with *Pseudoamictus* Bigot, from which it differs in having a more humped thorax, more globular head, more narrowed oragenal recess, less widely separated antennal segments, narrower genae, narrower interocular space in females, long contact distance of male eyes. He considers *Amictogeron* Hesse a transitional genus between *Geron* Meigen and *Pseudoamictus* Bigot.

The species of *Amictogeron* Hesse are restricted to South Africa.

Length: 3.5 to 7 mm.; wing 4 to 7 mm.

Head, lateral aspect: The head is globular, the occiput extensive and swollen and with scattered, rather scanty, shaggy pile and bristles; in females the occiput is prominent above and below, in males only below, rapidly flattening and receding near the vertex; there is no central cavity, no indentation. The front is rather flattened. A small quadrate depression immediately in front of the antennae bears scattered, stiff, bristly hairs on the upper half which are curled forward. The ocellar tubercle is rather strongly swollen, the ocelli occupying an obtuse triangle with a cluster of 4 or 5 erect bristles. The face, without pile, thinly pollinose, is short in profile, shorter in males, its height is little more than the thickness of the first antennal segment; the antennae rest on the eye margin in lateral aspect, hence the face is not greatly different from the obtusely flattened face of *Geron* Meigen, the surface is pollinose and has 2 or 3 minute hairs.

The lower sides of the oragenal cup and genal area have long, matted, shaggy, flattened hairs directed upward along the sides of the eye; postmargin of the entire eye. The proboscis is long and slender, arising from the bottom of the head and extending forward and is at least twice as long as the head. The palpus is long, but so thin as to be threadlike. The antennae are long and slender, especially the first and third segments. The first segment is 5 or 6 times as long as wide and at least 6 times as long as the short, beadlike second segment. The first segment bears numerous, rather long bristles along the lateral and ventral margins, which are longer

and more conspicuous basally; second segment with a few setae laterally at the apex. The third segment is more narrow than the second, straight, nearly cylindrical, and of almost uniform thickness to the apex. Near the apex it becomes strongly narrowed, the sharp apex bears a minute conical spine; inner margin of the third segment with short, suberect setae.

Head, anterior aspect: The head is very short oval, the head nearly as wide as the thorax, the eyes in the male are extensively holoptic for about four-fifths the distance of antennae to ocelli; the line of contact is sunken and the upper facets larger. In the female the eyes are rather strongly separated by somewhat less than in *Geron* Meigen. The ocellar triangle is small, equilateral, and prominent with vertical sides and bears several erect bristly hairs. The vertex is very little wider in the female than the ocellar triangle. The front is small and rhomboidal. The antennae are separated at the base by almost the thickness of one segment. The oragenal cup is ventral in position leaving the face long beneath the antennae, more than half as long as its width. The oragenal cup is quite deep, narrowing anteriorly, truncate beneath the face with the inner walls quite steep and the genal space extensive from the anterior view and bearing a dense tuft of long, shaggy, matted pile directed forward; tentorial fissure or pits absent.

Thorax: The mesonotum is rather strongly humped; it has both erect, long, coarse dark pile intermixed with erect, fine, pale pile and also curled, flat-appressed, glittering hair, nowhere obscuring the ground color. In contrast to *Geron* Meigen, there is always some black pile present. Bristles absent. The scutellum is large, unusually long and exceptionally thick and convex with abundant long pile similar to the mesonotum. The humeri and mesopleuron, sternopleuron and pteropleuron have abundant long fine pile; posthypopleuron with only a few fine, somewhat shorter hairs, metapleuron apilose.

Legs: The legs are quite slender and have scales on the hind femur with an anteroventral fringe of moderately long bristly hair that is rather fine; tibiae and tarsi exceptionally slender and elongate, the hind pair with 8 quite short dorsomedial bristles and 4 or 5 still shorter anteroventral bristles. The anterior tibia has 5 or 6 extremely short, ventral bristles on the outer half, still shorter ones anteriorly; pulvilli well developed.

Wings: The wings are iridescent and hyaline, the subcostal cell yellow, veins pale brown; both first and second veins are nearly straight; the radial sector is short and ends well before the end of the second basal cell; the first and second posterior cells and discal cells gradually diverge. The anterior crossvein is at the middle of the discal cell. The anterior branch of the third vein arises in an oblique, rounded curve almost exactly at the midpoint of the first posterior cell; the remainder of that vein is plane and ends at the apex of the wing. There are 3 posterior cells, the anal cell is closed and shortly stalked, the axillary lobe is large, the

alula small, the ambient vein complete; marginal villi moderately long.

Abdomen: The abdomen is short, a little longer than the thorax and somewhat compressed laterally; it is distinctly pinched and compressed laterally. There are 9 segments that may be seen from above, the eighth is shorter and exposed chiefly laterally. The pile of the abdomen is quite scanty but long and bristly and slender and erect.

The pile is intermixed, with which on the dark pilinose background is some scanty, short, curled, shining, somewhat flattened and appressed pile. Female terminalia simple, surrounded by long, bristly hairs on edges of tergites.

Male terminalia very complex and variable between species; of 21 species, Hesse (1938) figures 15; I summarize the comments of Hesse on terminalia in this fashion: like *Geron* Meigen in having the basal part single, not divided into two symmetrical halves by dorsal suture or depression. The greater part of the dorsum is membranous, marked off by a chitinous strip on each side passing into the more rigid chitinous sides; bristly hairs if present placed dorsally on chitinous part; the basal part passes apically into a flattened, lobelike or lappetlike apical process on each side corresponding to the true dististyli (beaked apical segments) of Bombyliinae; these lobes or processes, as in *Geron* Meigen, are not hinged and movable as in the Bombyliini; they are usually flattened, lappet or triangularlike, not boss or fingerlike as in *Geron* Meigen; dorsally each apical process usually has an adpressed spine, at their bases there is ventrally a single spine or recurved process, or a projecting spined process. The medial aedeagal complex is placed in the basal part, attached on each side toward apex by a ramus; the sides of that part joining onto the ramus usually prolonged into a flap or lobe.

The prolongation of this lobe assumes various forms of taxonomic value; on each side the ramus is usually produced apically into a straplike, hooklike, or spine-like process, into a strongly recurved spine or even more complex figure. The ramus on each side meets or is joined onto a medial, central guide, not so well defined as in *Geron* Meigen, which surrounds or into which passes the middle part of aedeagal complex and there may be one or more additional spinelike processes.

Material available for study: The series in the British Museum (Natural History) and also males and females of *meromelas* Hesse sent by Dr. Hesse for study and dissection.

Immature stages: Unknown.

Ecology and behavior of adults: Hesse (1938) found one species settling upon flowers of *Mesembryanthemum* sp.

Distribution: Ethiopian: *Amictogeron anomalus* Hesse, 1938; *barbatus* Bezzi, 1921; *basutoensis* Hesse, 1938; *bezzii* Hesse, 1938; *capiculus* Hesse, 1938; *cheliciterus* Hesse, 1938; *consors* Hesse, 1938; *dasyceirus* Hesse, 1938; *disparilis* Hesse, 1938; *fuscipes* Hesse,

1938; *karooanus* Hesse, 1938; *lasiocornis* Hesse, 1938; *leptocerus* Bezzi, 1921; *marshalli* Hesse, 1938; *meromelas* Hesse, 1938; *montanus* Hesse, 1938; *namaensis* Hesse, 1938; *nigrijemoris* Hesse, 1938; *peringueyi* Hesse, 1938; *phacopteris* Hesse, 1938; *waltoni* Hesse, 1938.

Genus *Pseudoamictus* Bigot

FIGURES 103, 311, 548, 555, 862, 863, 864

Pseudoamictus Bigot, Ann. Soc. Ent. France, ser. 7, vol. 2, p. 342, 1892. Type of genus: *Amictus heteropterus* Wiedemann, 1821, not Macquart, by original designation.

Pseudempis Bezzi, Ann. South African Mus., vol. 18, p. 94, 1921. Type of genus: *Amictus heteropterus* Wiedemann, 1821.

Hesse (1938), pp. 960-962, key to 3 South African species.

Curious, blackish flies with brown or gray pollen and with mostly brownish or reddish golden pile that is fine, wiry, partly appressed and upon the whole, rather scanty. The size is larger than the species of *Geron* Meigen and the form somewhat more elongate; the abdomen tends to be cylindroid rather than strongly tapered as in that genus. There is a curious, theravid-like appearance; the head is subglobose and the antennae are elongate. The first antennal segment is as long as the remaining two, strongly widened or swollen, progressively toward the base and the two segments lie adjacent and bear considerable, long, fine, dense, subappressed pile on all sides except the medial aspect; the second segment is beadlike, the third segment progressively tapered to a narrow bristle-tipped apex. The face is extensive ventrally and obliquely and has pollen only but the wide gena bears a conspicuous, vertical, dense, forwardly directed band of stiff, shaggy, or bristly hairs.

The wings are rather long and slender and uniformly tinted with reddish-brown villi. The anterior branch of the third vein arises rather abruptly, and after making a broad, basal arch forward, extends in nearly a straight line to the wing apex. The vein closing the discal cell is strongly sigmoid, the discal cell much longer anteriorly than posteriorly. The anterior cross-vein enters the discal cell at or beyond the middle and the anal cell is closed in the margin. As Hesse (1938) notes, there is a tendency for the base of the second submarginal cell to be opposite the apex of the discal cell. It is notable that the eyes in the male are separated, much separated in the type-species. The gena is much broader than *Geron* Meigen or *Amictogeron* Hesse. The male terminalia like the other flies in this subfamily are quite complex; they are much like *Amictogeron* Hesse; it has a single undivided basimere, ending apically on each side in an apical, lappetlike process, directed obliquely, and provided with a dorsal spine.

The few species are entirely South African in distribution.

Length: 5 to 12 mm.; of wing 5 to 12 mm.

Head, lateral aspect: The head is globose, with the face extensive, produced forward a little more than half the length of the eye. It is distinctly sloping beneath the antenna, slightly convex, blunt at the anteriormost ledge above the oragenal cavity. From the lower part of the face, the oragenal cavity slopes obliquely backward. The gena is very wide, and bears conspicuous, long, rather dense, tufts of coarse, bristly, reddish-golden hair or weak bristles, arising near the eye margin well below the middle of the eye and extending as a brush obliquely upward along the sides of the oragenal cavity. The ground color of the entire head is black or brownish black, but completely obscured everywhere by a fine, gray pollen. The occiput is prominent but only toward the middle of the head. It is especially extensive ventrally and is also prominent even below the eye. It slopes gradually inward lengthening all the while, and there is no deep interior cup as found in the division Tomophthalmae. Viewed from above there is no fissure or lobe behind the vertex. The ocelli rest upon a conspicuous, rather high, compact tubercle and are attached to the sides of this tubercle. The posterior ocelli lie behind the eye margin. The occiput is coarsely sub-punctate where the sparse pile arises. Outwardly the pile is long, rather fine, stiff but wiry, but the more medial pile is long, matted, coarse, and golden. A fine, wiry, black pile on the upper half of the head extends well beyond the eye margin, although none of it arises at the eye margin. The matted yellow pile scarcely extends beyond the eye margin.

There is not even a depression behind the short column of the ocelli tubercle. The palpus is remarkably filiform and, contrary to the statement of Hesse, it appears to be bent in such a way that there is a distinct long, nearly bare basal segment followed by a longer, equally slender, slightly curved, short, fine, bristly pilose, apical segment. The entire length of the palpus is less than that of the first antennal segment. The proboscis is slender and from extreme base to apex it is only $1\frac{1}{2}$ times as long as the rather long head. The labellum is likewise slender. The antennae are conspicuous and elongate; the first segment is especially long; it is widest and somewhat swollen basally from the point of attachment, and it is as long as the next two segments together, and very hairy on all sides except medially. The medial surface is covered by fine, gray pollen. The hair or pile of the first segment above, below, and laterally is long, rather dense, coarse, bristly, subappressed and reddish brown, extending above to the end of the second segment. The second segment is short and bead-like and of about the same width as the narrowed apex of the first segment. The first segment is only gradually narrowed. The second segment is truncate apically but rounded at the base, and there are a few, short setae. The third segment is a little shorter than the first, of the same width as the second segment, nonannulate from the lateral aspect, with parallel sides on the basal sixth; it then begins to narrow to just beyond the

middle where there is a slender, attenuate, stylelike portion quite narrow at the apex, but with a very minute spine.

The pile of the first antennal segment, at least where it rises from the base, is almost as long as the third antennal segment.

Head, anterior aspect: The head is slightly wider than the thorax, oval, with the oragenal and the genofacial space rather rapidly widening below. Below the antenna this space is almost a third of the head's width; at the bottom of the head, it is at least half the head's width. The genae are well-developed below the eye, they are very wide, and the shallow oragenal cup is narrow with a vertical shining clypeal strip in the middle, margined by a narrow, thin, yellowish sidewall of no great depth, on the outside of which is a shallow crease that appears to be part of a tentorial fissure; lateral to this is another pale yellow ridge ascending to the wide pollinose gena. In males the eyes are separated by the width of the ocellar tubercle: in the females the interocular space on the vertex is not broader than twice the width of the ocellar tubercle. Hesse notes that the front of the male is larger, broader, and longer than either *Geron* or *Amictogeron* Hesse. The front in the male is distinctly depressed medially on the lower half above the antenna and extends rhomboidally between the base of the antenna, the segments of which are narrowly separated. Yet, because they extend medially toward each other, they almost touch throughout most of their length. The second and third antennal segments extend obliquely outward and the third segment is conspicuously annulated only when viewed from above.

The upper eye facets are somewhat more coarse and enlarged and distinctly arranged in a circular pattern on each side of the front. The posterior eye margin is quite plane throughout, and there is a very faint, impressed crease on the occiput separating off the bare marginal portion of the occiput which bears no pile.

Thorax: The thorax is slightly compressed laterally and a little convex on the mesonotum but not conspicuously so. The whole thorax is brown or brownish black with a light reddish or sepia-brown pollen. The pile is scanty, straggly, and scattered, rather dense or abundant laterally, but nowhere obscuring the ground color. There are two types of hair: a long, stiff, shining-yellow, curled, erect or partly erect hair, more abundant on the anterior third and slightly more in front of the scutellum, and especially abundant on the lateral margin, forming extremely weak, slender bristles, perhaps no more than bristly hairs on the notopleuron, the postalar callosity, and on the margin and disc of the scutellum. The convex, opaque, brown pollinose, scutellum is almost as long as wide. It forms perhaps more than a hemicycle. Its pile is scanty. The humeral pile is very much like that of the anterior mesonotum. The pleural pile is quite scanty, except dorsally on the mesopleuron where it is loose and more abundant. While the whole pleuron is pollinose and opaque, the ptero-

pleuron, the metapleuron, and the metanotum are bare; the hypopleuron has a few, long scattered hairs beneath the very large haltere which has a curiously elongate knob. The squama has a scanty fringe of fine hair.

Legs: The legs are quite slender and comparatively elongate. The anterior femur has a few stiff, long hairs ventrally near the base. The middle femur has a complete fringe of long, stiff hairs ventrally and similar short hair anteriorly. The hind femur has a ventral lateral fringe of more scanty, long, stiffened hairs. All the femora have scattered, flat-appressed, yellowish, flattened, scalelike hairs. All three pairs of tibia have a few spicules near the apex. Middle tibia with 4 short, stout, spinous setae ventrally at the apex and hind tibia with a circle of at least 12 black spicules on the ventral half. All tarsi long and slender. Ventral spicules are more conspicuous on the hind tarsus. Claws slender, the pulvilli long and spatulate. The arolium acute at the apex.

Wings: Large, much longer than the abdomen and uniformly tinted with brown a little wider at the base, and with a rather distinctive venation. The third vein is slightly arched backward to end well below the apex of the wing. The anterior branch of the third vein arises first rectangularly, then makes a broad curve and is plane throughout much of its length and ends at the wing apex. The anterior crossvein is oblique and enters the discal cell just beyond the middle. There are only 3 posterior cells and the vein closing the discal cell is very strongly sigmoid. Anal cell narrowly open or closed in the margin. The axillary lobe is comparatively wide, but the alula narrow; ambient vein complete. The base of the costa is thickened for a short distance and there is a weak costal comb of oblique setae, with a flattened basal scale without hook.

Abdomen: The abdomen is elongate and comparatively slender with a tendency for the sides to be compressed and it is at least nearly twice as long as the mesonotum, the scutellum excepted. The abdomen is dark, brownish black, opaque, with a yellowish-brown pollen, the eighth tergite is rather light orange brown. The second tergite is a little longer than the next two tergites. The seventh tergite is only apparent laterally. The pile on the side of the first tergite is long, stiff, erect, and golden, but rather scanty. All the remaining tergites except the last one have some scattered, more or less erect, fine, long, yellow hairs together with somewhat more abundant, still scanty, appressed, curled, slightly flattened golden hairs. The rather large terminalia are directed straight backward, or posteriorly, and are fairly complex, with accessory prongs and spurs, which are shining brown or brownish black. Dr. Hesse describes the male terminalia in the following way:

The hypopygium is very much like of *Amictogeron* Hesse. Like that genus it has a single, undivided basal part, ending apically on each side in a lappet-like lobe, which is provided dorsally with a spine as in *Amictogeron* Hesse; with the strongly chitinous strand on each side from base of each apical

lappet-like process (which passes) obliquely to the side, sometimes provided with a strong, apically directed spine. The ramus on each side is produced apically into a strap-like process of a bifid process. The central, guide-like part, which abuts on the bases of the rami, with or without an apically directed prong placed on each side and situated dorsal to the aedeagus.

The male terminalia from dorsal aspect, epandrium removed, show a compact, elongate-oval structure in which the dististyli are short, attenuate, and with a rather strong, divergent, curved, hornlike tip. In addition there are no less than 3 pairs of accessory processes, which in this work we term claspers, and these prominent strong, curved, hornlike processes lie dorsal to the epiphallus and aedeagus. From the lateral aspect all of these structures emerge from a single undivided basistylus, and the long flattened leaflike ramus is likewise

attached laterally to the basistylus, and is extended obliquely upward on each side of this clasper-complex. The epandrium is large, oval, pointed apically, leaf-shaped, extended almost directly upward, and bears very large cerci.

Material available for study: I am indebted to Dr. A. J. Hesse of the South African Museum, Capetown, for the loan of a male of the type-species.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Pseudoamictus bezzii* Paramonov, 1930 [= *heteropterus* Bezzi, not Wiedemann]; *heteropterus* Wiedemann, 1821 (as *Amictus*), also (as *Pseudempis*, Bezzi, 1921); *luctuosus* Bezzi, 1921 (as *Geron*).

Subfamily Usiinae Becker, 1912

Small flies which are readily recognized in the type-species by the short thorax and scutellum, the short, very broad, compact abdomen that is much wider than the thorax, the long slender proboscis, the presence of only 3 posterior cells with anal cell always closed and stalked; also the pilosity everywhere is minute, appressed, and setiform. The head is small, much more narrow than the thorax. The cheeks and midlateral face are reduced to a mere line. The greatly swollen occiput is convexly rounded outward to the eye margin, and possessed of a sharply delimited, laterally placed, welt-like, vertical bulla (occipital schwielen of authors); these characters delineate the type-species of the genus. However, there are other species placed within the genus that do not have the occipital bullae. Also, in the past some genera have been placed in this subfamily which have 4 posterior cells, such as *Legnotomyia* Bezzi.

Usia incisa Wiedemann has all the above characteristics except that the pile of front, face, cheeks, occiput, thorax, abdomen, and legs is long, fine, dense, and erect; the abdominal tergites are lined behind with yellow, the face and cheeks are wide laterally and the occiput is poorly developed and lacks the lateral bullae. Generally speaking this species is so similar to species of *Legnotomyia* Bezzi it could easily be mistaken for that genus, except that the venation of the distal part of the radial field is so aberrant in *Legnotomyia* Bezzi, which moreover has 4 posterior cells and very widely open anal cell.

There are so many interesting examples of remarkable convergence in superficial appearance among members of different genera of bee flies that, despite the strong suggestive resemblance of *Legnotomyia* Bezzi to species of the Usiinae, like *Usia incisa* Wiedemann, I reject the idea of any close relationship between them, in spite of the very heavy veins shared by both. Not only does *Legnotomyia* Bezzi have 4 posterior cells, it has a very different type of antenna and a well-developed face below the antenna, and a different type of hypopygial development. I agree with Bowden that *Pusiella* Paramonov finds its real relationship with the *Corsomyia* Wiedemann species. *Psiatholasius* Becker I place in synonymy under *Legnotomyia* Bezzi. I raise *Corsomyia* Wiedemann to tribal status within the Bombyliinae.

Consequently, I restrict the Usiinae to those flies with 3 posterior cells and the other peculiarities outlined above.

Besides *Usia* Latreille and the subgenus *Parageron* Paramonov there are left in this subfamily three other genera: *Oligodranes* Loew and *Apolysis* Loew, and I place *Dagستانia* Paramonov near here. I have not

seen that genus; Paramonov likens it to *Geron*, *Parageron*, and *Oligodranes*. As for *Geron* Meigen this genus is very different from all these others, and, as Hesse has shown, it amply deserves separate subfamily status. The relationships of these genera, especially *Oligodranes* Loew, is very close to *Usia* Latreille.

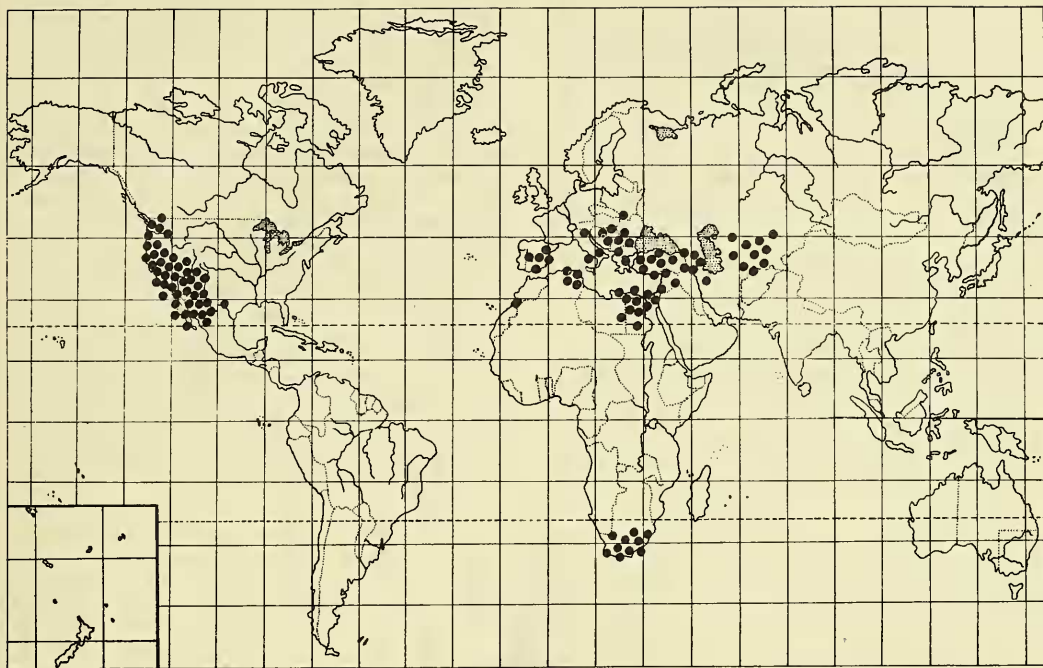
I have before me a species of *Usia*, which clearly falls into the subgenus *Parageron* Paramonov.

Melander (1946) has ably discussed the relationship of European type-species of *Oligodranes* Loew and *Apolysis* Loew to their American counterparts; he points out that the European species of both have 2-segmented palpi, whereas the American counterparts have a single segment. He notes that were this character of the number of segments of the palpus regarded as of generic significance, then the American species of *Oligodranes* Loew would fall into *Rhabdoselaphus* Bigot, and the American species of *Apolysis* Loew would require a new name. Hesse (1938) notes that many genera with apparently unisegmented palpus show a plane of separation when treated with potash. Melander further notes that the curious occipital bullae, shared by *Usia* Latreille and *Parageron* Paramonov although not present in all species of either genus, is also present, but not in all species of *Oligodranes* Loew; there are intergrades. Hence, with Melander, I leave all known species of today in *Oligodranes* Loew and *Apolysis* Loew, and *Usia* Latreille, and *Parageron* Paramonov. It seems apparent, as Melander has pointed out, the unisegmented condition of the palpus is a reduction of the palpus from an earlier multisegmented condition, and that *Apolysis* Loew was derived from *Oligodranes* Loew by the loss of the posterior crossvein. And of course it is possible that *Usia* Latreille, a Mediterranean genus, was derived from *Legnotomyia* Bezzi, also a Mediterranean genus, by the loss of a posterior cell; this may well be true.

Melander (1946) found 37 new species of *Oligodranes* Loew in intensive collecting within mountain canyons of the West, the restriction of habit suggesting, in the case of *Oligodranes* Loew (and the very different *Mythicomyia* Melander), a rather youthful taxon.

The Usiinae show a curious, very short, broad figure with several peculiar genera. In *Apolysis* Loew the basal part of the aedeagus is large and bulb-shaped, attenuate, and extended apically. The basistyli are small, the dististyle very large with sharp angles and hooks and with a conspicuous, deep, dorsoapical incision from the lateral aspect. However, these characteristics are entirely lacking in *Oligodranes* Loew. On the whole *Usia* Latreille and *Parageron* Paramonov and *Apolysis* Loew are much more alike than is *Oligodranes* Loew.

Usiinae



TEXT-FIGURE 28.—Pattern of the approximate world distribution of the species of the subfamily Usiinae.

KEY TO THE GENERA AND SUBGENUS OF USIINAE

1. Occiput usually rather strongly swollen, although gradually rounded inwardly and regularly sloping inward from the eye margin. In consequence of the thickness of the occiput the vertical groove or fissure behind the ocelli is prominent. Sides of lower occiput usually with conspicuous vertical ridge of some width. Abdomen wide, more or less sub-spherical, or subglobose and convex, and at least, short oval. These flies are rather bare, short pilose for the most part, often with a somewhat denuded appearance. Third antennal segment obtuse at apex, with subapical dorsal spine. Flies ranging from 2 mm. rarely, to 10 mm. rarely 2
Occiput not exceptionally swollen behind and hence the post ocellar, vertical fissure not prominent. Abdomen conical and tapered, either long or short. Third antennal segment variable. Flies ranging from minute, three-fourths of a mm. to 4.5 mm. 3
2. Occiput much more poorly developed, less prominent, more flattened; postocellar fissure shallow. Eyes holoptic in male and in contact for a considerable distance and ommatidia on upper three-fourths of male eye, much enlarged and clearly separated from lower facets. Hypopygium generally less swollen . . . *Usia* (*Parageron*) *Paramonov*
Occiput more prominent and usually conspicuously pilose, although the pile is not usually long. Postocellar fissure deep and narrow. Lamellae of epipygium (male hypopygium) grossly swollen, capsular, and conspicuous. Eyes of both sexes widely separated, the ommatidia alike in males *Usia* *Latreille*
3. The discal cell is complete *Oligodranes* *Loew*
Discal cell is confluent with the second posterior cell, the medial crossvein being absent *Apolysis* *Loew*

Genus *Usia* Latreille

FIGURES 78, 79, 312, 545, 556, 852, 853, 854

Volucella Fabricius, Entomologica Systematica, vol. 4, p. 412, 1794. Type of genus: *Volucella florae* Fabricius, 1794. Designated by Latreille, 1802. Error in spelling by Geoffroy, Syrphidae (*Volucella*), 1764. Officially rejected under opinion 441.

Usia Latreille, Hist. nat. Crustacés, pt. 3, p. 430, 1802. Change of name.

Volucella Meigen, Klassifikation Beschreibung Insekten, vol. 1, p. 194, 1804, not Geoffroy, 1764.

Parageron Paramonov, Trav. Mus. Zool. Kieff, no. 6, p. 127, 1929c. Type of subgenus: *Parageron orientalis* Paramonov, 1929, by monotypy.

Becker (1906), pp. 196-201, key to 26 males and 27 females of Palaearctic species.

Séguy (1926), pp. 228-229, key to 9 species from France.

Engel (1933), pp. 63-66, key to 30 Palaearctic species.

Austen (1937), p. 55, key to 7 species from Palestine.

Efllatoun (1945), pp. 200-202, key to 13 species from Egypt.

Paramonov (1947c), pp. 207-220, revision, treating many species.

Paramonov (1950), pp. 342-351, key to world species of *Usia*.

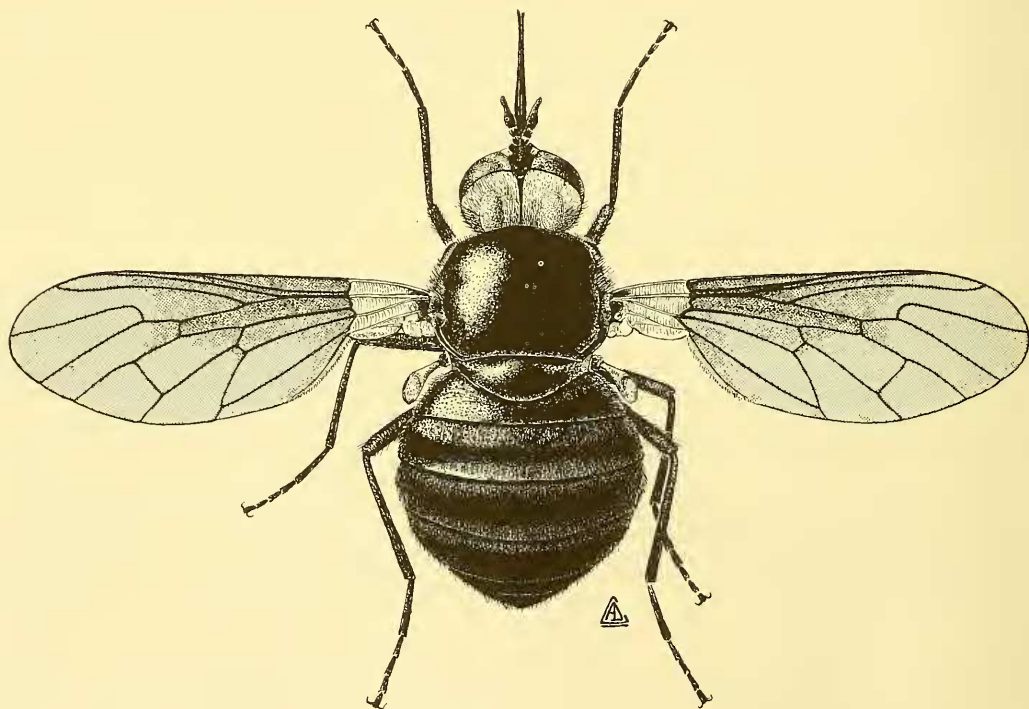
Curious flies of very compact, robust form. Most species are rather small. The abdomen is wider, sometimes much wider than the thorax and the flies have

either a very bare, denuded appearance as in the type-species, due to the minute appressed setae of the thorax and abdomen, or have long, fine, erect, comparatively dense, pale pile on these areas, as in *Usia incisa* Wiedemann; hence the appearance is variable, but it is always compact. Eyes always holoptic in males, except the species *ignorata* Becker.

These flies have only 3 posterior cells; the anal cell is closed and petiolate and there are only 2 submarginal cells. The veins are strong and stout. Anal cell closed. The proboscis is elongate and slender. The tibiae and femora have fine-appressed setate pile and may have microscopic scales. Male terminalia very prominent and much protruded and conspicuous.

The occiput is never cupulate or hollowed out centrally or bilobed above. Nevertheless, it is peculiar that the occiput in the type-species is so very much swollen and that it bears below on each side a curious, vertical bulla, a thing lacking in some species; this structure is also found in certain species of the genus *Oligodranes* Loew, and sometimes in *Apolysis* Loew.

Usia Latreille is restricted to the Mediterranean and the North African regions. Efllatoun (1945) recorded 13 species from Egypt, 9 of them undescribed.

TEXT-FIGURE 29.—Habitus, *Usia aenea* Rossi.

Length: Often minute; length of body as little as 1.4 to 3.2 mm., or as much as 8 to 9 mm., excluding proboscis of 3.5 to 4.5 mm. Wing length may reach 7 mm.

Head, lateral aspect: The head is globular, the occiput variable. In males of some species it is greatly reduced in extent immediately behind the vertex, growing more and more prominent ventrally with rounded, convex, sloping sides reaching to the eye margin. The whole occiput is pollinose and covered with rather dense, long, coarse pile outwardly subappressed, the pile becoming shorter toward the vertex and longer in the middle and below. In females, as in the type-species, however, the upper occiput is extensive and swollen dorsally, very rounded and convex and perhaps even a little more extensive than on the lower part of the head. It is also pollinose but with shorter, abundant, relatively short, stiff, erect pile. In both of these types of occiputs the halves are separated below the vertex and the ocellar tubercle marked by a distinct, narrow fascia or sulcus. In the female type-species the posterior ocelli are actually behind the posterior eye corners, and this is due to a recession or curving forward of the eye. The front is either polished and bare with some pollen or micropubescence laterally, and a few short, oblique setae, or may be wholly pollinose, a little inflated, with comparatively dense, long, fine, erect pile. Likewise the face itself varies.

In the type-species the face, as well as the front, is very short in profile, the former restricted to a small triangle on each side just below the base of the antennae, and extended as a mere line down to the middle of the eye. The oragenal cup extends completely to the antennae and because of its dorsal width and breadth occludes the face laterally as well as dorsally. The face margin below the antennae is barely visible in profile as a line along the eye margin. However, in *Usia incisa* Wiedemann both face and front, oragenal cavity and gena are very extensive from the lateral aspect. However, in this species also the oragenal cavity reaches quite to the base of the antennae. The eye is large in *Usia* Latreille with the upper facets twice the size of those below and the posterior eye margin is plane.

The proboscis is very long and quite slender, 2 to 3 times as long as the head, the labellum is even more slender and is about as long as the third antennal segment. Palpus in the type-species minute, cylindrical, quite slender with tiny additional clublike segment at the apex bearing 2 or 3 long hairs. In *Usia incisa* Wiedemann the palpus is large, the second segment strongly clubbed with numerous bristly hairs over the whole surface. The antennae are attached at the upper third of the head, they are relatively short, but slender, the first two segments are nearly equal, both bearing a few setae dorsally in the type-species and in *Usia incisa* Wiedemann the first segment bears numerous, long, coarse, bristly hairs directed forward and outward on the upper half of the segment with shorter pile below. The third segment in this species is a little longer than the first two segments combined, of about the same

width though slightly narrowed toward the narrowed apex, and it bears a shallow, spoon-shaped depression at the apex, and also has 4 or 5 long, oblique setae or short bristles dorsolaterally on the outer half. The antennae of the type-species are similar, the third segment is somewhat more robust on the basal half and the spoon-shaped apical depression bears a distinct short, but stout apical spine.

Head, anterior aspect: The head is distinctly wider than high viewed from the front. In the males it is so much broader below that it sometimes appears hemi-circular with a rounded dorsal portion, and with the genofacial area steadily widening below. Males strongly holoptic, the front sometimes swollen above the plane of the eye, so that in length the front may be shorter than the eye from the point where it is joined to the posterior eye corners. Ocellar tubercle a little swollen, the large ocelli lie in an equilateral triangle and rest on the eye margin in the male. Front of female in the type-species not quite twice as wide as the width of the ocellar tubercle, which actually lies behind the upper eye corners. And in the type-species the sides of the genofacial area are nearly parallel, being only slightly wider below. The antennae are distinctly separated at the base but curve inward to nearly or quite touch at the end of the first segment. In the type-species the oragenal cup is deep especially opposite the proboscis, but slants forward and upward to the antennae. The inner walls are not vertical but are strongly sloping, and in this species the gena is reduced to a narrow line. In *Usia incisa* Wiedemann the oragenal cup is much more shallow and both face and gena quite extensive. It has a small tentorial pit just opposite the proboscis.

Thorax: The thorax is very short and broad, wider than long, rather evenly convex and while not greatly humped both head and abdomen are somewhat decumbent. The pile in the type-species is comparatively dense, short, bristly or setate and curled either upward or backward. The large, wide scutellum, including its posterior margin, is similarly pilose. Lateral and anterior margins of the mesonotum with dense, microscopic, glittering, appressed, scaliform pile, somewhat pollen-like in character. Humerus bordered above with similar pile and its whole surface bearing erect, bristly hairs like those of the mesonotum. In other species the mesonotum may have pollinose vittae, the scutellum may be strongly inflated across the middle, nonrugose and the whole mesonotum and scutellum with dense, long, matted pile. There is similar long pile on almost the whole of the mesopleuron. In the type-species the whole of the pleuron is pollinose and the upper half of the mesopleuron bears stiff, bristly pile, which is somewhat similar to that on the sides of the mesonotum and only slightly longer. Postalar callosity broad and flattened, the lateral ridge on the posterior half bears numerous, bristly hairs. All the remaining pleuron is without pile in the type-species but a few of the more pilose species may have a few hairs on the metapleuron and upper sternopleuron. The metanotum is extremely short and

lacks pile. The squama is large with a fine, scattered fringe of hairs. Halteres are large and short with an unusually large club.

Legs: The legs are stout and relatively short. All of the femora equally but not conspicuously thickened; they are rather more thickened in the type-species which bears rather abundant, appressed, stiff setae with a few slightly longer, stiff, semierect hairs below. Also the femora are shining and rather bare; ground color green black in the type-species. In other species they are covered densely with minute, rounded, microscopic, appressed scales. Tibiae stout but more slender than the femora and clothed with quite abundant, much appressed setae but without outstanding bristles or spiculate setae. The tarsi are relatively short with shorter setae similar to those of the tibiae. Pulvilli large and prominent, widely spatulate, the claws fine and sharp.

Wings: The wings are comparatively wide with stout veins and in the type-species the wing is a little narrowed toward the base with narrow alula and the axillary lobe is no wider than the third basal cell. In other species the alula is much wider and the axillary lobe is also much wider than the third basal cell. Wing always with 2 marginal cells and 3 posterior cells, each of them widely open. The anterior crossvein enters the discal cell either just before or just beyond the middle. The second vein arises upward from the end of the radial sector. The anterior branch of the third vein arises steeply and rectangularly in the type-species with strong outward bend, but in other species it sometimes arises quite gradually. The vein closing the discal cell in the type-species is plane and rectangular, in other species a little curved and oblique. Anal cell closed, the stalk long or short. Ambient vein complete. Villi almost continuous and coarse. Wing usually tinted quite diffusely along the veins; in one species, wings spotted. First vein sometimes rugose.

Abdomen: The abdomen is large, much wider than the thorax and about $1\frac{1}{2}$ times as long. It is very slightly convex across the middle but the tergites are narrowly rolled over laterally. It is widest at the end of the second segment, the second to fourth tergites being practically equal in length, the fourth tergite is only slightly more narrow. The fifth, sixth, and seventh tergites when viewed from above represent an obtuse triangle, and the second, third, and fourth tergites have a nearly complete, transverse, foveal depression near the end of the tergite. Other species lack such depression and have the abdomen somewhat more narrow. In the type-species the pile of the abdomen is rather dense, flat-appressed and setate, very little longer along the sides, and the whole surface is conspicuously rugose, or pitted; the color is uniformly shining greenish black. While there are 8 tergites in both male and female the eighth is extremely short and may be recessed beneath the seventh. Some species have the tergites nonrugose, nonfoliate, but with sublateral depressions in the middle, and each of the 8 tergites bears conspicuous, opaque, linear, yellow postmargins and the pile is comparatively

dense, long, fine, and erect and thus in much contrast to the type-species. Female terminalia simple, without spines. The male genitalia are generally large, protruded and conspicuous. The hypopygium often forms a very large, bulblike expansion, directed downward. The dorsal lamella, paired and bipartite, is sometimes segmented at the apex; the ventral, bilobed, and fused pair of lamellae has the upper margin often emarginate or showing several pairs of obtuse teeth; between the ventral lamellae there is a pair of hooks in some species; the recessed and hidden penis (aedeagus) occupies a position between and in front of these hooks.

Material studied: The type-species and several other species.

Immature stages: Xamben (1898) gave a short description of larvae and pupae but with no illustrations. See discussion under life histories.

Ecology and behavior of adults: Efflatoun Bey (1945) records having captured most of the smaller Egyptian species feeding on flowers of desert Compositae, such as *Astericus*, *Sonchus*, *Centaurea*, *Senecio*, *Calendula*, *Launaea*, *Picris*, as well as on *Zilla spinosa*. He states that the adults are excellent hoverers.

Distribution: Palaearctic: *Usia accola* Becker, 1906; *aenea* (Rossi), 1794 (as *Bombylus*) [= *florea* Meigen not Fabricius, 1804]; *aeneoides* Paramonov, 1950; *angustifrons* Becker, 1906 [= *putilla* Becker, 1906]; *anus* Becker, 1906; *atrata* (Fabricius), 1798 (as *Volucella*) [= *florea* Schiner, 1868, not Fabricius, = *puberula* Loew, nomen nudum in litt. et in coll., = *vicina* Macquart, 1840]; *aurata* (Fabricius), 1794 (as *Volucella*) [= *taeniolata* Costa, A., 1884], *aurata loewii* Becker, 1906; *bicolor* Macquart, 1855; *calva* Loew, 1869; *carmelitensis* Becker, 1906; *claripennis* Macquart, 1840; *crinipes* Becker, 1906; *deserticola* Efflatoun, 1945; *efflatouni* Venturi, 1945 [= *bicolor* Efflatoun, 1945, not Macquart, 1855]; *elbae* Efflatoun, 1945; *engeli* Paramonov, 1950; *flavipes* Efflatoun, 1945; *florea* (Fabricius), 1794 (as *Volucella*) [= *cuprea* Macquart, 1834, = *gagathea* Bigot, 1892]; *foveipata* Brullé, 1832; *grata* Loew in Rosenhauer, 1856; *grisea* Efflatoun, 1945; *ignorata* Becker, 1906; *incisa* (Wiedemann), 1830 (subg. *Parageron*) [= *major* Macquart, 1840]; *incognita* Paramonov, 1950; *inornata* Engel, 1932; *lata* Loew, 1846; *manca* Loew, 1846; *minuscule* Efflatoun, 1945; *notata* Loew, 1873; *novakii* Strobl, 1902 [= *pusilla* Macquart, 1840, not Meigen]; *pallens* Becker, 1906; *parvula* Efflatoun, 1945; *punctipennis* Loew, 1846; *pusilla* Meigen, 1820; *sicula* Egger, 1859 [= *florea* Loew, 1846]; *similis* Paramonov, 1950; *syriaca* Paramonov, 1950; *tevfiki* Efflatoun, 1945; *tomentosa* Engel, 1932; *transcaspica* Paramonov, 1950; *unicolor* Loew, 1873; *vagans* Becker, 1906; *versicolor* (Fabricius), 1794 (as *Volucella*) [= *hyalipennis* Macquart, 1840]; *vestita* Macquart, 1849; *ornata* Engel.

Oriental: *Usia marginata* Brunetti, 1909; *sedophila* Brunetti, 1909.

Subgenus *Parageron*

Engel (1933), in his key to the species of the genus *Usia* Latreille, incorporated all of those species known to him that fell into Paramonov's taxon *Parageron*. After studying his examples that clearly fall into the subgenus *Parageron*, I agree with Engel that the only valid differences lie in the holoptic eyes of *Parageron* and the relatively smaller hypopygium, the features of which I have summarized from the dissection of this individual that was collected in Spain. Because this specimen was destroyed in return shipment from my technician, I was unable to effect a determination of this species. Nevertheless, it met all of the requirements of *Parageron*.

The male terminalia from dorsal aspect, epandrium removed, show a very broad short structure, somewhat similar to *Apolysis* Loew, except that there is a distinct bridge across from each ramus crossing over the epiphallus. The dististyli are curious, flared, leaflike structures with a thick apical process; this structure with apparently enclosed duct ends in a curious, soft, sponge-like structure. The dististyli are strongly flared and divergent laterally. Basistyli blunt and truncate apically. The epandrium large and subquadrate. Laterally the dististyle has a rather deep ventral incision.

Distribution: Palaearctic: *Usia (Parageron) grisea* Paramonov, 1947; *incisa* Wiedemann, 1830 [= *major* Macquart, 1840]; *lutescens* Bezzi, 1925 [= *orientalis* Paramonov, 1929]; *lutescens minor* Eflatoun, 1945; *turkmenica* Paramonov, 1947; *zimini* Paramonov, 1947.

Genus *Apolysis* Loew

FIGURES 81, 329, 332, 549, 560, 855, 856

Apolysis Loew, Öfvers. Kongl. Vet. Akad. Forhandl., vol. 17, p. 86, 1860. Type of genus: *Apolysis humilis* Loew, 1860, by monotypy.

Paramonov (1931), p. 201, treatment of Palaearctic species.

Engel (1933), pp. 128-129, key to 3 species.

Hesse (1938), pp. 849-851, key to 7 species from South Africa.

Melander (1946b), pp. 458-459, key to 9 species from the western United States.

Minute flies, black in general color, or rarely in part yellow. They are strongly humpbacked but less conspicuously than in *Mythicomyia* Coquillett. Grayish pollinose for the most part, they often show spots or vittae upon the mesonotum. The abdomen is usually short and wide, wider than the thorax, often with narrow, yellow postmargins on the tergites. The pile is fine, erect, generally quite scanty and sparse. The proboscis is about twice as long as the subglobular head; the occiput is prominent only below but may show lateral, weltlike bullae similar to those in some species of *Oligodranes* Loew and *Usia* Latreille. The moderately lengthened antennae have a similar apical pit with spine dorsally placed on the third segment.

These flies are most closely related to *Oligodranes* Loew, from which they are quickly separated by the absence of the discal cell, the crossvein normally closing the discal cell having been lost by specialization. Likewise, the palpi are reduced in American species to one segment by fusion.

Apolysis Loew is primarily a Holarctic genus with several species found in South Africa. In the Old World they are found in the North African and Mediterranean regions as well. All known American species are from California.

Length: 0.75 mm. to 3 mm.

Head, lateral aspect: The head is subglobular but in males the upper part of the occiput is much reduced and is reduced to a thin line behind the ocelli, rapidly widening backward and downward to the point of attachment of head to thorax below the middle of the head. This upper profile of the occiput is plane. The eye is rounded below and recedes forward a little below the middle. The eye is very large occupying most of the lateral aspect of the head. The facets on the lower part of the eye are much smaller than the very large facets above, but there is a more or less gradual transition. The front is extended forward considerably beyond the eye margin. The antennae are attached above the middle of the head; the frontal area is almost as long as the lateral genofacial area. The face itself, in the middle, beneath the antennae, seems to be almost eliminated by the oragenal cavity which extends almost to the antenna. Both face, front, and genae are densely micropubescent. The front has 3 or 4 long, suberect, stiff, bristly hairs on each side near the middle and there is a fringe of still longer, isolated, erect, slender, though stiff, hairs running from near the base of the antennae down the sides of the face and gena, forming several loose rows below and continued over the whole area beneath the eye. The occiput has a sublateral fringe of moderately long, scanty, scattered, bristly hairs and this patch is continued medially almost to the foramen. The posterior surface is scaliform microsetate and the long setae are present over the whole of the occiput, except beneath the ocelli. Posterior margin of the eye entire and plane from the ocelli to the division point of the facets.

The proboscis is elongate, relatively slender, wholly micropubescent with a few fine, short, stiff hairs both above and below, with a rather small labellum. The proboscis extends forward and is about $1\frac{1}{2}$ times as long as the head. The palpus is elongate and slender and not very large. It appears to be composed of 2 segments with the apical segment slightly thicker and bearing apically and dorsally 5 or 6 moderately long setae hairs. The antennae are attached at the middle of the head; they are elongate, and about two-thirds as long as the head. The first segment is beadlike, widest apically, longer than high at the apex and the same length or slightly longer than the second segment. Second antennal segment beadlike, a little wider than the first and both of these segments with 2 or 3 short setae

dorsally at the apex. The third segment is flattened, long oval, nearly twice as long as the first two segments, rounded at the apex, the lower margin not quite plane, the whole surface micropubescent and dorsally near the apex. It has a concave incision bearing a short, stout spine.

Head, anterior aspect: The head is as wide or a little wider than the thorax. The face and front are not separated. In the female the front is wide with a slight depression across the middle. It is wholly pollinose and has a few, widely spaced, more or less erect, stiffened hairs. The eyes in the male are in contact for more than half the length from ocellus to antennae. The antennae are narrowly separated. The ocellar tubercle is high and conspicuous, the very large ocelli lie in an equilateral triangle and rest against the eye margin in the male. The oral opening is quite large, elongate oval, extending almost to the base of the antennae and is rather deep. The genae are wide and together with the interior of the oragonal recess are entirely micropubescent, with long, fine, scattered, erect pile on the genae only. The oragonal cup is restricted to a narrow linear strip on the lower half of the oral opening, separated by a distinct tentorial fissure. There is a small hollow in the occiput posteriorly above the junction of the head with the thorax. There are no flanges or tubercles.

Thorax: The mesonotum is high and equally convex and humped anteriorly and posteriorly. The mesonotum is loosely covered with rather long, scanty, fine, erect hairs, and the rather thick, short, convex scutellum has similar scattered discal hairs. Notopleuron without noteworthy bristles or setae. Humerus with 2 or 3 long hairs. The entire thorax is black with usually opaque black vittae and most of the mesonotum and all of the pleuron is densely covered with bluish white or gray or brownish yellow, dense, somewhat scalelike micropubescent. Upper part of mesopleuron with a few scattered hairs. Remainder without any pile, except the micropubescent. Squama rather large and long with a loose fringe of long hairs. Halteres with a large, short oval, closed knob.

Legs: The legs are rather slender, moderately long, the anterior tibia with several rows of short, suberect setae, a little longer and more conspicuous posteroventrally. Anterior femur slightly swollen toward the basal half with a row of short, erect setae above and scattered, long, bristly hairs posteriorly. Middle legs rather similar to the first pair, the femur more slender. Hind legs with the femur much more slender and covered with minute micropubescent that appears scalelike. This femur also has some short, subapressed setae dorsally and medially and has a fringing row laterally and another one ventrally, of rather long, erect, stiff or bristly hairs. Hind tibia quite slender with a dorsal row of bristly hairs similar to that of the femur, perhaps denser and containing 4 long elements in the middle. It also contains several shorter bristly hairs at the base and 1 or 2 at the apex and also a lateral

row of 5 or 6 similar hairs that are not quite so long, together with additional, short, medial, and ventral, suberect hairs. It also has micropubescent. Pulvilli large, long, curved and spatulate, the slender claws bent sharply at the apex.

Wings: The wings are relatively large with weak veins. There are 2 submarginal cells, the anterior branch of the third vein arises gradually midway from the wing apex to the anterior crossvein. The whole second submarginal cell is narrow. There are only 3 posterior cells and no discal cell. Anal cell closed with a comparatively long stalk. Axillary lobe broad. Acula large and wide. The ambient vein lies shortly beyond the end of the third vein, the anterior crossvein lies opposite the angulate end of the second basal cell.

Abdomen: The Abdomen is somewhat elongate, about as wide as the thorax or a little more narrow. It is narrowed toward the apex, is generally opaque black, except on the first segment which may be grayish and the pile is fine, long, loose and scattered, and erect, especially along the sides. The abdomen in some species has a great deal of white or yellow color on it. In still other species the posterior margins of the tergites may be linearly whitish. It is much shorter and somewhat appressed along the posterior margins of the tergites. I find 8 segments on the abdomen. The male hypopygium is rather large and forms a troughlike bowl ventrally in which the genitalia lie.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium of males with the inner apical angle or part of basal parts considerably produced and prominent, spinulated apically and acting as a sort of guide to the aedeagus; aedeagus also much produced beyond basal parts, lying along middle of scoop-like and conically produced last sternite; beaked apical joints small and provided on the inner side with a membranous, flattened process or flap, sometimes quite broad.

The male terminalia from dorsal and lateral aspect, epandrium removed, show a short, wide, obtuse figure with broad, laterally extensive dististyli which bear several strong, hornlike or tuberclelike processes. The aedeagus and the ejaculatory process extend outward as a long slender process well beyond the strongly divergent dististyli. The position of the dististyli may be an artifact. The basistyle is rather small, though wider basally. The epandrium is quite large, dwarfing the remainder of the structure and completely enclosing the basal apodeme.

Material studied: I have before me paratypes of several species.

Immature stages: Unknown.

Ecology and behavior of adults: Melander (1946) records taking these flies at flowers of *Cryptantha intermediate* and *Eriophyllum confertiflorum*, also of a *Phacelia* sp., and upon *Eriodictyon crassifolium*. All were taken in May in the southern part of California. Hesse (1938) records South African species from in or on the corolla tubes of the red-flowered *Mahernia grandiflora* in the Karoo.

Distribution: Nearctic: *Apolysis aperta* Melander, 1946; *disjuncta* Melander, 1946; *druivas* Melander, 1946; *glauca* Melander, 1946; *minutissima* Melander, 1946; *mohavea* Melander, 1946; *petiolata* Melander, 1946; *timberlakei* Melander, 1946.

Palearctic: *Apolysis andalusica* Strobl, 1898; *cinerea* Perris, 1839; *eremophila* Loew, 1873.

Ethiopian: *Apolysis brevivittis* Hesse, 1938; *cingulata* Hesse, 1938; *funalis* Hesse, 1938; *humilis* Loew, 1860; *lindneri* Hesse, 1962; *maherniaphila* Hesse, 1938; *thornei* Hesse, 1938; *xanthogaster* Hesse, 1938.

Genus *Oligodranes* Loew

FIGURES 77, 231, 338, 550, 552, 553, 554, 737, 857, 858

Oligodranes Loew, Stettiner Ent. Zeitung, vol. 5, p. 160, 1844.

Type of genus: *Oligodranes obscuripennis* Loew, 1844, designated by Becker, 1913, p. 484.

Rhabdopsclaphus Bigot, Bull. Soc. Ent. France, ser. 6, vol. 6, p. ciii, 1886a. Type of genus: *Rhabdopsclaphus mus* Bigot, 1886, by monotypy.

Pseudogeron Cresson, Ent. News, vol. 26, p. 201, 1915a. Type of genus: *Pseudogeron mitis* Cresson, 1915, by original designation.

Paramonov (1929), M. A. Sc. Ukr., vol. XI, p. 190, treatment of Palearctic spp.

Engel (1933), p. 136, key to 4 Palearctic species.

Melander (1946), pp. 463-470, key to 57 Nearctic species.

Small flies, sometimes black, polished and shining with yellow borders upon the posterior margins of the tergites; in many other species the general black coloration is heavily modified by dense, brown or silvery-gray pollen, which if it acquires any grease quickly eliminates the patterns upon the thorax and abdomen. These flies are of about the same size range and general appearance as *Phthiria* Meigen and have only 3 posterior cells. They resemble *Phthiria* Meigen in several other respects, such as the broad wing base and alula, the long, slender proboscis, the holoptic males and the obliquely flattened and appressed aspect of the upper eye and front; besides this both *Phthiria* Meigen and *Usia* Latreille have very large, terminal genitalia. Moreover, the antennae are somewhat similar in type but with a differently placed apical spine. A point of similarity between some of the species of *Oligodranes* Loew and the Mediterranean genus *Usia* Latreille is the presence of the curious occipital bullae; while it is possible that these flies were derived from remote *Phthiria*-like ancestors by the loss of one posterior cell, it is more likely that they were derived at one time from a *Legnatomyia*-like fly. Efflatoun (1945) illustrates a wing of *Phthiria salmayensis* Efflatoun in which the entire distal section of the second branch of the medius has dropped out, leaving the wing with only 3 posterior cells in this particular individual.

The genus *Oligodranes* Loew is represented by a very few species in the region of Asia Minor, 2 species from South Africa, and 52 species from the United States.

Length: 1.25 mm. to 6 mm. with most species about 3 mm. in length.

Head, lateral aspect: The head is globular and tends to be elongate. The occiput in the female is extraordinarily swollen and bulbose though more prominent on the lower half, convex and sloping sharply outward and forward to the eye margin. In the male it is much more reduced above though still prominent below. The pile is rather dense, fine, and erect, and in males it becomes a rather long fringe along the upper eye borders. The front is flattened in the female on the upper half and plane with the eye but both face and front extend well beyond the eye margin and the lower front is therefore slightly elevated but rather flat. The front of the male is similar to that of the female, but the eyes are much flattened so that the upper half of the eye is distinctly triangular. Posterior eye margin entire and nearly plane; the upper eye facets enlarged. The face has minute, erect setae scantily distributed along the sides, the surface pollinose. In the males this pile is rather longer and more conspicuous, and likewise erect.

The proboscis is quite long and slender, 3 or 4 times as long as the head in most species but not quite twice as long in *Oligodranes sigma* Coquillett. The palpus is rather slender, not very long, although it extends slightly beyond the face. It appears to consist of a short, basal segment and a long, setate, clavate, apical segment which bears some short, fine, bristly hairs below. The antennae are attached near the top of the head at about the upper fifth or sixth. They are comparatively large, the first segment is cylindrical, 4 or 5 times as long as wide, the second segment beadlike, shorter than wide, and approximately one-fourth or one-fifth as long as the first segment. The first segment has some rather conspicuous fine, erect bristles dorsally, as long or longer than the width of the segment and a few others shorter below. The third segment is characteristically broadly oval and somewhat flattened, narrow at the base and minutely attached, then rather rapidly but evenly widening above and below. This segment is more or less long oval, a little plane on the upper surface, strongly convex below and dorsally at the apex it is concave and "hollowed out." At the bottom of the concavity it bears a very short, conical, pubescent microsegment.

Head, anterior aspect: The head is much more narrow than the thorax. In the male the eyes are strongly holoptic, touching and depressed at the junction for a distance equal the length of the front. Actually the front sends a narrow, wedgelike triangle posteriorly in between the eyes for a short distance. The ocellar tubercle is comparatively low, small, equilateral, the ocelli resting on the eye margin. In the female the eyes are rather widely separated. The ocelli do not touch the eye margin and the vertex is half the width of the front at the antennae. The antennae arise narrowly separated by less than the thickness of the first segment. The oragenal recess is curious inasmuch as it begins far back at the bottom of the head, though not as far back as the rounded, posterior eye corners; then it curves steeply and vertically upward, wide and extremely deep,

and reaches quite to the base of the antennae. This anterior upper portion is triangular with the inner walls steep and even curled over a little. All of this lateral portion in front of the head is probably to be interpreted as lateral face, for near the bottom of the eye there appears to be a separate, low, marginal border going upward and disappearing, which probably represents the remnant of the gena. I find no trace of the tentorial fissure.

Thorax: The thorax is a little longer than wide, the mesonotum low and only slightly convex. They vary from species in which the mesonotum is almost entirely shining black and the abdomen similar, but with narrow postmargins, to other species in which the thorax and abdomen, even though black, are heavily coated with grayish white pollen. The pile varies from minute, very scanty and short and partly appressed to the group of shining black species which may have abundant, comparatively dense, erect pile over the thorax, the scutellum, and the mesopleuron. Remainder of pleuron and metanotum without pile and usually pollinose. The humerus bears a few scattered hairs or dense, long, pile in the more heavily pilose species, and pile of the scutellum is generally like that of the mesonotum. Sternopleuron sometimes pilose. Squama large with a fine fringe of pile, knob of halteres large, stalk rather short.

Legs: The legs are of no great length, the femora are a little thickened. In pilose species they are rather densely covered with erect, fine pile changing to appressed setae near the apex of the middle and especially the hind pair. In the less pilose species the femora are apt to be pollinose and covered only with scattered, short, stiff, semierect setae, with their tibiae similar in both respects. Tarsi are slender, the pulvilli are broadly spatulate apically, extending nearly to the apex of the relatively short, rather blunt claws, which are strongly curved at the apex.

Wings: The wings are hyaline with the base broad. There are only 3 posterior cells, all widely open. The anterior branch of the third vein arises in a rather low or gentle arch. There are only 2 submarginal cells and the anterior crossvein enters the discal cell slightly before or slightly after the middle. The anal cell is closed with a long stalk; the crossvein closing the discal cell is either plane and rectangular or shows a somewhat sigmoid curve indicating a double origin for this vein. Also, the first longitudinal vein may end rather nearer to the end of the auxiliary vein than to the end of the second vein. Axillary lobe broad basally, the alula comparatively wide. The ambient vein may end at the first posterior cell or at the anal cell.

Abdomen: The abdomen is rather broad at the base as far as the end of the second segment. It may be a little wider than the mesonotum or not quite as wide. In length it is as long as the length of the thorax including the scutellum or sometimes a little shorter. The abdomen may be only as long as wide, nearly circular, viewed from above with all of the tergites, except the first and second, much shortened or it may be elongate

conical, somewhat compressed laterally, each tergite narrowed progressively. The species are greatly variable in point of pile present varying from those with only a few subappressed, setate hairs arranged in 1 or 2 transverse rows to other species that are covered with long, erect, rather dense, fine hairs on both tergites and sternites. The female genitalia are surrounded by a fringe of pile, no spines being present. Male terminalia small and short and barely protruded beyond the eighth tergite.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium of male based on that of *O. namaensis* n. sp., very small with the outer apical parts or angles of basal parts broad and triangular; beaked apical joints somewhat flattened and with short bristles or setae; aedeagal or middle part with the lateral struts almost vestigial, very small, the basally directed strut more or less lobe-like, with the aedeagus short and apparently in form of two stylet-like processes, the aedeagus produced basally and above middle part into an aedeagal strut on each side; lateral ramus on each side from basal parts joined on to apical aedeagal part.

The male terminalia from dorsal aspect, epandrium removed, show a very short, quite wide, obtuse figure, with the base of the aedeagus and the epiphallus forming curious, short, broad, apically hemicircular plate, all lying far forward. The ejaculatory process seems to be paired or divided. From the lateral aspect the dististyli are small but slender, forming an apical toothlike process. The basistyle is attenuate apically, but very much widened basally, almost completely obscuring the basal apodeme.

Material studied: Several North American species collected by the author, and material in the National Museum of Natural History, the British Museum (Natural History), and the Department of Entomology of the University of California.

Immature stages: Unknown. I have an individual of *Oligodranes cinctura* Coquillett in which the whole posterior part of the abdomen has been eaten away by psocids; to the inner surface of the tergites there are the remains of large, elongate, oval, yellow eggs nearly one-third of a millimeter long. Anteriorly the ovaries show a great mass of very minute eggs.

Ecology and behavior of adults: These flies come to a variety of desert flowers. I have collected several species on flowers in New Mexico. Only one species is known from the eastern United States in temperate rainfall.

Distribution: Nearctic: *Oligodranes acrostichalis* Melander, 1946, *acrostichalis matutinus* Melander, 1946; *albopilosus* Cole, 1923; *analis* Melander, 1946; *anthonomus* Melander, 1946; *ater* (Cresson), 1915 (as *Pseudogeron*); *bicolor* Melander, 1946; *bifarius* Melander, 1946; *bilineatus* Melander, 1946; *bivittatus* (Cresson), 1915 (as *Pseudogeron*); *capax* (Coquillett), 1892 (as *Geron*); *chalybeus* Melander, 1946; *cincturus* (Coquillett), 1894 (as *Geron*); *cinereus* Melander, 1946; *cockereelli* Melander, 1946; *colei* Melander, 1946; *comosus* Melander, 1946; *dissimilis* Melander, 1946; *distinctus*

Melander, 1946; *divisus* Melander, 1946; *dolorosus* Melander, 1946; *eremitis* Melander, 1946; *fasciolus* (Coquillett), 1892 (as *Geron*); *formosus* (Cresson), 1915 (as *Pseudogeron*); *instabilis* Melander, 1946; *knabi* (Cresson), 1915 (as *Pseudogeron*); *lasius* Melander, 1946; *longirostris* Melander, 1946; *loricatus* Melander, 1946; *lugens* Melander, 1946; *maculatus* Melander, 1946; *marginalis* (Cresson), 1915 (as *Pseudogeron*); *mitis* (Cresson), 1915 (as *Pseudogeron*); *montanus* Melander, 1946; *mus* (Bigot), 1886 (as *Rhabdopselaphus*); *neuter* Melander, 1946; *obscurus* (Cresson), 1915 (as *Pseudogeron*); *palpalis* Melander, 1946; *panneus* Melander, 1946; *parkeri* Melander, 1946; *polius* Melander, 1946; *pulcher* Melander, 1946; *pullatus* Melander, 1946; *pygmaeus* Cole, 1923; *quinquenotatus* (Johnson), 1903 (as *Phthiria*); *retroversus* Melander, 1946; *scapularis* Melander, 1946; *scapulatus* Melander, 1946; *setosus* (Cresson), 1915 (as *Pseudogeron*); *sigma* (Coquillett), 1902 (as *Geron*); *sipho* Melander, 1946; *speculifer* Melander, 1946; *togatus* Melander, 1946; *trifidus* Melander, 1946; *trochilus* (Coquillett), 1891 (as *Geron*).

Palearctic: *Oligodranes flavus* Paramonov, 1929; *fumipennis* Loew, 1844; *hyalipennis* Séguin, 1941; *modestus* Loew, 1873; *obscuripennis* Loew, 1844; *rubriventris* Paramonov, 1936; *superbus* Engel, 1933.

Ethiopian: *Oligodranes elegans* Hesse, 1938; *flavipleurus* Bowden, 1964; *namaensis* Hesse, 1938.

Genus *Dagestania* Paramonov

Dagestania Paramonov, Trav. Mus. Zool., Kiev, no. 6, p. 133, 1929. Type of genus: *Dagestania pusilla* Paramonov, 1929, by monotypy.

Paramonov (1947), pp. 207-220, key to 2 species.

I have not seen the genus *Dagestania* Paramonov and I quote his description:

It is very close to *Geron* Meigen, *Parageron* Paramonov and *Oligodranes* Loew. Although I have seen only one somewhat damaged female, unfortunately, I have to set up a new genus for this type, since I am not able to classify it under any of the genera known up to now. This genus is distinguished from *Geron* Meigen in the following way: the first antennal segment is not cylindrical and not two and one-half to three times longer than the second, but only slightly longer; and both segments thicken toward the apex. Antennal pile is lacking (the third segment absent in my specimen). The very wide mouth cavity extends to the base of the antenna themselves, while in the case of *Geron* Meigen they definitely do not extend to it. Cheeks almost absent; cheeks very narrow. It is distinct from *Oligodranes* Loew because of the short, single segmented palpus.

From *Parageron* Paramonov it is distinct because the anal veins are closed off far from the edge of the wings, and because of the absence of thorax hairs or pile, etc. The usual crossein is clearly this side of the middle of the discal cell. Pulvilli are present. The structure of the front (frons) is unique.

Paramonov describes the type-species in the following words:

The basic color of the head is dark, only the very narrow cheeks and palpus are almost whitish. The whole head, with the exception of the front (frons), is whitishly dusted. The front (frons) is dusted gold yellow. The structure of the front (frons) is unique; almost at the end of the second third of its length there is a transverse groove, since the front at this point makes a distinct ridge to the base of the antenna. This elevation is three sided: the central triangular plate, which forms a distinct angle with the rest of the surface of the front, is dusted gold yellow, as the latter is; the lateral plates (also triangular), which gradually become the cheeks, are dusted white. The whole head is bare, only the occiput is weakly dusted yellowish. The occiput of the head bulges strongly backward. The posterior border of the eyes are without evagination (indentation). The edges of the front (frons) (stirnrand) viewed from the front, exhibits or takes on breakage or crack in the region where the cross groove is found, after which they diverge more than before.

The basic color of the thorax is dark; the back of the thorax is completely bare, and dusted yellow. On the middle there are two indistinct yellowish longitudinal stripes or vittae, which begin at the front edge and take up two-thirds of the length of the dorsum of the thorax. They are surrounded by a somewhat darker coloration and have a very narrow, dark separating stripe. Between the shoulders and the base of the wings there are a few shining hairs; (The sides of the thorax are bare, partly black and yellowish.) Scutellum dusted yellow, with eight protruding short yellowish bristles, which form a half circle; they are not on the back edge itself, but clearly on the surface of the scutellum. Legs yellow, microscopically pilose, without bristles. All the tarsal segments are black; front femur darkened. Metatarsus very long, almost equal to the length of the second, third, and fourth segments together; the second tarsal segment equal to the third and fourth segments together. Tarsi clearly longer than the tibiae. Haltere bright yellow. Wings transparent. Venation very similar to that of *Parageron* Paramonov but the anal cell is closed off far from the wing edge.

Back part of the abdomen completely yellow beneath, black on top, with narrow, yellow posterior margins on the segments; the pile consists of very short, sparse, dark hairs.

Body length 2.5 mm., wing length 2 mm.

1 female, 16. V. 26. Kumtorkale, Dagestan. Sande. Rjabov leg.

Specimen in Meier Collection

Material available for study: None.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palearctic: *Dagestania longirostris* Paramonov, 1947; *pusilla* Paramonov, 1929.

Subfamily Heterotropinae Becker, 1912

While I leave these flies all within the subfamily Heterotropinae, it is entirely possible that flies like *Caenotus* Cole and *Apystomyia* Melander, and others, should be placed in a separate family. I leave them in the Bombyliidae because there is so little difference in the venation from that of certain other bombyliids, with the exception that some of these genera have a forked fourth vein. In all the genera included here the eyes in the male are divided into a group of very small facets concentrated very low toward the bottom of the eye. One genus in the subfamily, *Caenotus* Cole, was removed from the Therevidae by Melander (1927); one species has 5 posterior cells and consequently can still be confused with the Therevidae; the proboscis in these

flies is very short indeed, fleshy and placed within the deep, triangular oral cup with its sloping sides.

The small, highly polished black flies in *Apystomyia* Melander are as black as shining pitch; their weak, milky wings and petiolate fourth vein are very peculiar. This genus is the same as *Alloxytropus* Bezzi who described it from Egypt (1925c); Efflatoun has re-described and nicely illustrated the Palaearctic species (1945). The largest genus is *Heterotropus* Loew, abundant in the Middle East, ranging into India, one species of which was described by Melander, collected on April 16 from flowers of desert marigold in Organ Pipe National Monument.

Heterotropinae



XENOPROSOPINAE

TEXT-FIGURE 30.—Pattern of the approximate world distribution of species of the subfamilies Heterotropinae and Xenoprosopinae.

The subfamily is separated from the remainder of the Bombyliidae by the simple posterior margin of the eye, nonindented, lower facets in male bisected into facets of much smaller size, much as in bibionids; tibiae without seriate spines, the third vein with two branches, and the anal cell petiolate; the occiput is flattened, the anal cell closed and petiolate. Many of these characters are shared by other bombyliids.

The venation is rather unique, the ambient vein lacking in *Prorates* Melander, and ending at the fourth vein in *Apystomyia* Melander. The veins are always dilutely hyaline with little or no pigment or wings milky. The

male genitalia are large, exposed, protruded, terminal, nonrecessed as is characteristic in so many lower Brachycera; female often with acanthophorites.

We are acutely in need of some knowledge about their life histories, immature stages, hosts if any, all of which we now lack.

This subfamily shows some relationship with both *Crocidium* Loew, and it might well be reduced to a tribe within the Bombyliinae.

I have been able to dissect males of only one genus, and the genitalia are described under *Heterotropus* Loew.

KEY TO THE GENERA OF HETEROTROPINAE

1. Flies with the characters of the subfamily, especially divided facets in eyes of male, tibiae without spines, anal cell closed and stalked, third vein forked, first posterior cell open, 4 or rarely 5 posterior cells, and proboscis distinctly projecting beyond the oral cavity 2
With all of the above characters but with the proboscis very short with fleshy labellum and completely confined to the sunken, wide, more or less triangular oral cavity with its sloping walls. Abdomen elongate and not with dense fur-like vestiture 3
2. The intercalary vein arises from the discal cell, between the fourth and fifth veins. Third antennal segment elongate, tapered, slender, style-tipped. Ambient vein present around hind margin of wing. Abdomen either obtuse, or long and tapered. Generally light-colored flies or if dark, with light

markings, paired, especially on the abdomen. Anterior face jutting forward as an almost or quite horizontal ledge. Feeds upon flowers *Heterotropus* Loew
The intercalary vein arises from the fourth vein. The second posterior cell is petiolate. Ambient vein absent. Third antennal cell conical with a small or microscopic style, weak flies; abdomen a trifle swollen toward the base.

Prorates Melander

3. Third vein branching near the discal cell; the second posterior cell is sessile; discal cell shorter than the basal cells; thorax opaque pollinose *Caenotus* Cole
Third vein branching near the apex of the wing; second posterior cell long petiolate; discal cell longer than the basal cells; whole body, especially thorax, shining pitch black. Wings milky *Apystomyia* Melander

Genus *Heterotropus* Loew

FIGURES 96, 527, 547, 774, 782, 785, 837, 838, 839, 976

Heterotropus Loew, Beschreibungen europäischer Dipteren, vol. 3, p. 182, 1873. Type of genus: *Heterotropus albidipennis* Loew, 1873, by monotypy.

Malthacotricha Becker, Ann. Mus. Zool. Acad. Imp. Sci., St. Pétersbourg, vol. 12, p. 312, 1907d. Type of genus: *Malthacotricha glauca* Becker, 1907d, original designation. Described as an Empididae.

Paramonov (1929), p. 127, treatment of Palaearctic species.

Séguy (1932), p. 130, key to 7 species.

Engel (1933), pp. 157-159, key to 23 species and subspecies.

Efflatoun (1945), pp. 73-75, key to 8 species from Egypt.

Rather bare, small flies with colorless wing veins and a strange division of the ommatidia into a sharply demarcated region of minute facets below and enlarged facets above; the eyes are very much enlarged in extent with the face correspondingly reduced. The body and head color tend to be largely whitish or pallid yellow, with sharp, blackish markings.

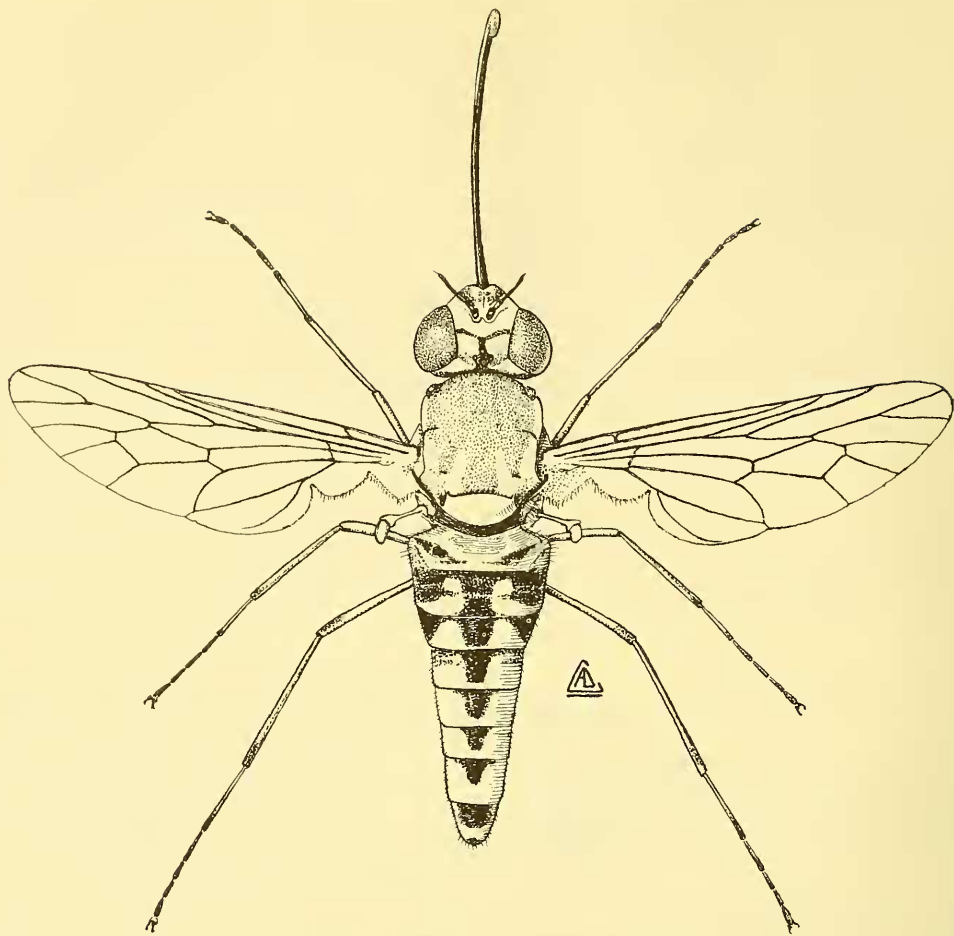
The deep oral recess is quite narrow, largely because the sides of the oral cup are so much widened. The antennae are elongate, slender, of nearly uniform thickness, except that the third segment is attenuate near the apex; the antennal pile is scanty; the first two segments are subequal in length. The entire fly has only fine, scanty pile, the scattered hairs inconspicuous but a little more numerous and appressed upon the abdo-

men. The anal cell of the wing is closed, all other cells are open; the position of the small crossvein varies, it may be near the middle of the discal cell with the latter drawn up angularly to meet it, or it may be at the outer third of that cell, or a little beyond. The wing tends to be a little narrowed though rounded at the apex with the anterior and posterior branches of the third vein ending about an equal distance above and below the wing apex. The marginal cell is quite narrow; the legs are without bristles; the scutellum has an impressed rim.

Heterotropus Loew is principally a Palaearctic genus largely confined to and characteristic of southern Europe and North Africa, and Egypt. However, there is a species from India, one from South Africa, with exaggerated extension of the face beneath the antennae, and Melander described one species from Arizona.

Length: 4 to 4.5 mm., wing 3.8 to 4.5 mm. The largest species is *elephantinus* Séguy, only 5.5 mm., excluding proboscis.

Head, lateral aspect: The head is large, the eyes extraordinarily developed. In males in lateral aspect the occiput is restricted to the lower half of the eye where it is quite short but bears relatively short, moderately abundant, stiff hairs extending to within a short distance of the eye margin. What I consider to be the thickened wall of the very large, elongate, oragenal cup extends outward in profile on the upper part of the facial area almost immediately beneath the antennae as a shelflike ledge of varying length in different species



TEXT-FIGURE 31.—Habitus, *Heterotropus aegyptiacus* Paramonov.

and farther in males; in *indicus* Nurse it is extended only slightly farther than the end of the first antennal segment. In Egyptian species such as *Heterotropus stigmaticus* Bezzi it extended outward to the end of the second antennal segment or beyond.

The restricted face proper represents a flattened area or even slightly sunken area immediately beneath the antennae, which like the small triangular front is pollinose. The very extensively developed eye is sharply divided obliquely into an area of much small facets on the lower third in front and reduced to the lower fifth posteriorly. Above this section the facets are much larger. The male eye is in contact for only about one-

third of the distance from antennae to vertex. The frontal triangle, though relatively small, is long and there is also a small, long, vertical triangle in front of the ocellar tubercle. The posterior margin of the eye is entire, and there are a few, quite short, stout bristles on each side of the upper occiput behind the ocelli and a short distance on each side of the ocellar triangle. The proboscis is comparatively long and rather stout with somewhat fleshy, stout labella and extends either straight forward or is folded up into the long, narrow, quite deep oral recess between the thickened, inflated walls of the large oragenal cup. Palpus small, rather slender and short with a few fine, setate hairs laterally

near the apex. The front is very slightly raised above the eye margin and is flat. The antennae are attached at the upper third of the head, the first two segments are quite short, of about equal length and each a little widened and rounded apically with only scattered, minute hairs.

Head, anterior aspect: Head much wider than the thorax; the antennae are adjacent and touching, the ocellar tubercle is low, longitudinally grooved, and forms an equilateral triangle, and the very large ocelli rest on the eye margin. The oral opening is quite large and occupies almost all of the space ventrally between the eyes; its walls are low, very wide, rounded laterally, protrusive to a varying extent, obliquely furrowed anteriorly, infolded and rounded medially. The actual oral opening is long, narrow, and deep. The genae are extraordinarily narrow and sunken along the eye margin and the shallow, tentorial fissure lies on its medial aspect, but the genae expand at the very bottom of the eye as a rather wide triangular area. Viewed from posteriorly the occiput is concave, its lower, outer lateral portion a little inflated.

Thorax: The mesonotum is only moderately high, more convex anteriorly, gently sloping behind, largely greenish or yellowish white in color and opaque with opaque black or brownish vittae on the mesonotum. The pile of the mesonotum is very scanty, fine and erect, and partly subappressed. The entire lateral margin of the notopleuron, however, bears loose, scattered, fine, long hairs. Transverse suture curiously deep and conspicuous. The pleuron is likewise semiopaque white and also bare, not pollinose; mesopleuron with short pile above; remaining pleuron everywhere bare. Scutellum with rounded, impressed margin and moderately abundant, short, erect pile. Squamae with a short fringe. Halteres large, the knob large, elongate and closed.

Legs: The legs are short, the femora a little thickened, especially the hind pair, generally entirely pale in color with the tarsal segments more or less blackish. The anterior tibia has only fine, short pile and 2 or 3 slightly longer hairs below. The anterior femur is almost bare, with a few fine, short, scattered hairs; middle legs similar; hind femur with a dorsal and medial fringe of fine, scattered hairs in length about equal to the apical width of the femur. Laterally and ventrally the hind femur has scattered, rather short, suberect setae; this hind femur is straight in shape. The hind tibia is as long as the femur with a ventral row of 10 or 12 fine, erect, bristly hairs of no great length and a dorsolateral row of 12 or 15 similar more oblique, bristly hairs and additional fine pile; there is also a dorsomedial row of short, suberect setae. The pulvilli are long and rather slender, claws sharply bent at the apex.

Wings: The wings are colorless; the veins are colorless. The costa and subcosta have a slightly yellowish tinge. The costa is expanded basally and has a distinct basal comb; what corresponds to the basal hook is blunt, triangular, and pilose. The second submarginal cell is

relatively short and the fork of the third vein is not very wide. The wing is more or less pointed or narrowed apically. There are 4 posterior cells. The anterior cross-vein enters the discal cell near the outer fifth and all of the posterior cells are widely open. The intercalary vein is long; discal cell elongate and widened apically and the anal cell is closed with a relatively short stalk. The axillary lobe is quite broad and the rounded alula is rather wide; ambient vein absent.

Abdomen: The abdomen is as long or longer than the thorax, tends to be rather flattened, greenish or yellowish white in color, especially apically, laterally, and on the sternites. There is often a pattern of black, medial, continuous or discontinuous spots on the middles of the tergites. I find 7 segments present in the male with the last one quite short. The hypopygium is large and club-like, obtuse apically. The abdomen has scattered, rather scanty pile, more or less setate, and in the material before me retrorse, except that along the side margin, there is a fringe of fairly abundant, long, coarse, more or less erect pile.

The male terminalia from dorsal aspect, epandrium removed, show a curious type of epiphallus which is sleeve-like basally with flared and expanded, narrow prongs distally; these overlie a bridge across the top from the corresponding basistyli. The basal part of the aedeagus is far removed from the center and is small and egg-shaped, and there are 3 quite long, slender, ejaculatory processes that extend beyond the epiphallus in the center of the pygidium. The dististyli are curious and remarkable; they are quite long, club-shaped both basally and apically and concave and much reduced in width in the middle. The entire pygidium is remarkable for being quite oval and the basistylus has a dorso-lateral process. From the lateral aspect the epandrium is more or less triangular though somewhat swollen ventrally and distally. The curious dististylus has a long, apical, downturned hook and the general shape of the entire pygidium is different from other genera of Bombyliidae. In the axial system the epiphallus arises in a very strong acute arch from a curious, wide, proximally almost circular, flattened, conspicuous, basal, winglike process.

Material studied: A male of *Heterotropus indicus* Nurse, a gift of the British Museum (Natural History), and a female of *Heterotropus aegyptiacus* Paramonov, sent me through the courtesy of Cairo University, Cairo, Egypt.

Immature stages: Unknown.

Ecology and behavior of adults: Efflatoun (1945), who with his assistants has probably captured more species than anyone, notes that he has only found them during the hottest hours of the day, from 1 to 4, the temperature above 45°C in the shade, a strong south wind. He found them on flowers of *Zygophyllum*, and small desert Compositae, and on flowers of *Statice*. Melander captured his species on flowers of desert marigold, and *Baileya multiradiata*.

Distribution: Nearctic: *Heterotropus senex* Melander, 1950.

Palaeartic: *Heterotropus aegyptiacus* Paramonov, 1929; *albidipennis* Loew, 1873 [= *sulphureus* Paramonov, 1929, female], *albidipennis sudanensis* Becker, 1922; *ammophilus* Paramonov, 1929; *arenivagus* Paramonov, 1929, *arenivagus chiraensis* Paramonov, 1929, *arenivagus flavoscutellatus*, Paramonov, 1929, *arenivagus normalipes*, Paramonov, 1929, *arenivagus repeteki* Paramonov, 1929; *atlanticus* Séguy, 1930, *bisglaucus* Bezzi, 1925; *bourdariesi* Séguy, 1938; *elephantinus* Séguy, 1929; *fulvipes* Séguy, 1932; *glaucus* Becker, 1907; *gussakovskiji* Paramonov, 1929; *hohlbecki* Paramonov, 1946; *kazanovskiji* Paramonov, 1925; *longitarsus* Séguy, 1930; *maculatissimus* Villeneuve, 1932; *maculiventris* Bezzi, 1925 [= *teufiki* Paramonov, 1929]; *magistrostris* Bezzi, 1926; *monogolicus* Paramonov, 1946; *nigrimanus* Séguy, 1931; *sabulosus* Paramonov, 1926, *sabulosus nigratarsis*, Engel, 1933; *stigmaticus* Bezzi, 1926; *trotteri* Bezzi, 1916; *xanthothorax* Eflattoun, 1945; *zarudnyi* Paramonov, 1946; *zimini* Paramonov, 1929, *zimini monticola* Paramonov, 1929.

Ethiopian: *Heterotropus munroi* Bezzi, 1926.

Oriental: *Heterotropus indicus* Nurse, 1922; *pallens* Nurse, 1922.

Genus *Caenotus* Cole

FIGURES 108A, 574, 697, 867, 868

Caenotus Cole, Proc. U.S. Nat. Mus., vol. 62, art. 4, p. 14, 1923.

Type of genus: *Caenotus inornatus* Cole, 1923, by original designation.

Melander (1950b), p. 148, key to all known species.

Small flies which were once placed in the Therevidae from which they differ in the second basal cell being pointed apically, the crossvein absent, the absence of bristles, and the short antenna. They are blackish, slender flies with soft, attenuated easily distorted abdomen; the pile of the body is very scanty, fine, and erect though a little more abundant upon the mesonotum. The anal cell is closed but with a short stalk; the first and second branches of the medius arise separately from the discal cell with a very short vein of varying length separating them. The ambient vein, though present, is weak. The first two segments of the antennae are quite short; the third segment is much widened from the base to the middle, then much narrowed and with a short microsegment that is as wide as the apical part of the segment. The eyes are divided into small facets below, large facets above.

Known only from New Mexico, southern Arizona, and California.

Length: 4 to 6 mm.

Head, lateral aspect: The head is approximately hemispherical; in males the occiput does not extend beyond the eye on the upper half and is actually somewhat concave on this portion. In the female the occiput

is somewhat similar but extends a little higher toward the vertex and in both sexes it is only moderately developed below the middle and toward the bottom of the head. From the lateral aspect the eye covers almost the entire head and in most specimens the face and front can barely be seen and sometimes in other specimens not at all. The oragenal cup or opening is deeply recessed into the triangular genofacial space, its pile is rather abundant but fine, loose and scattered, long, and extending downward and outward and largely restricted to the lower fourth of the head. Pile is absent below the antennae, except for a continuation of the minute, grayish micropubescence present upon the sides of the front; it continues below the eye to cover all of the gena to the eye margin and all of the oral recess as well. The long, fine pile continues around and upon the occiput on the lower third of the head and on the upper part of the occiput there is, very close to the eye margin, a row of scattered, fine, bristly hairs. The posterior margin of the eye is entire and extends medially inward on the upper half and viewed laterally it is clearly divided, but without a groove or colored line, into an area of minute facets on the lower third, and much larger facets above as in some bibionids.

The proboscis is very short and stout, with a short, stout labellum scarcely extending out from the lower part of the oral opening. Palpus, rather large, with rather numerous, long bristles, and composed of 3 segments. The front is small, flat, somewhat depressed medially in females and with micropubescence only, the middle bare. The antennae are small, the first segment is a little longer than the second which is beadlike, both of these bear several fine bristles dorsally and ventrally; these bristles are nearly equal in length to the vertical width of these segments. The third segment is of about the same length as the first two segments together, and while somewhat flattened laterally, it is angularly widened in the middle to an equal extent above and below, and apically it bears a large, short, flattened microsegment to which is attached a minute, apical microsegment. The antennae are attached a little below the middle of the head and just above the line on which the eye facets are divided into small and large groups.

Head, anterior aspect: The head is a little wider than the thorax; in males the eyes are holoptic and meet extensively, although the medial edge of each is strongly rounded leaving the frontal triangle narrow above and leaving the vertex composed entirely of the large, protuberant ocellar tubercle. In females the front is wide, it begins to be wider and flared outward on the lower third, and its width below the ocelli is more than one-fourth the total head width. As in males, the ocellar tubercle forms a prominent equilateral triangle, but unlike males it is well separated from the posterior eye margin. The ocelli are large. The oral opening is triangular, comparatively large, recessed and only moderately deep. The genae are wide, sloping inward and ap-

pear to have only very minute micropubescence. The tentorial fissure is barely evident.

Thorax: The thorax is comparatively high and moderately humped both in front and behind. The prothorax is very short, the vestiture consists of rather abundant, long, quite fine, erect, stiff pile covering the entire mesonotum and the humerus and continued onto the pronotum and as a middle band vertically down the mesopleuron and the sternopleuron, extending as far as the coxa. The sternopleuron and the entire metapleuron and the hypopleuron have only minute, sparse, micropubescence; all pleural pile more delicate than that on the mesonotum. Scutellum with abundant pile similar to that on the mesonotum but longer. Squama with a fine, delicate fringe. Halteres with a quite large, thin-walled, elongate, cup-shaped knob.

Legs: The legs are relatively short and slender, the femora, however, are slightly thickened. Anterior tibia with fine, abundant, subappressed pile only. Anterior femur with a fringe of numerous, long, stiff hairs below in several rows. Middle femur and tibia similar, the latter with a few, short, bristly hairs. Hind femur with abundant, subappressed, shining pile above and laterally and medially, but with the more sparse, short, scattered pile below, among which are 4 or 5 slightly longer, fine, stiff hairs. The hind femur is distinctly arched outward when viewed from above. The hind tibia has 2 or 3 very weak bristly hairs of no great length ventrally and the same number dorsally. Pulvilli long and spatulate. Claws fine and curved slightly at the apex.

Wings: The wings are weak but relatively large and rather wide apically as well as basally. The second submarginal cell is long and narrow, the anterior branch of the third vein forms a narrow fork with the posterior branch. The anterior branch ends a short distance above the apex of the wing. There are 4 posterior cells, all widely open, and the anterior intercalary vein is short. It is worth noting that the anal cell is closed with a long petiole or stalk. The axillary lobe is broad and the rounded alula is relatively narrow. The ambient vein is complete, but like all of the posterior veins behind the radius, it is quite pale. The anterior crossvein enters the discal cell slightly before the middle; this cell is of a peculiar shape, angulate below, short in length, and rather broad across the middle.

Abdomen is peculiar, elongate, tapered, with 8 tergites and sternites and a large, conspicuous, elongate, somewhat clublike hypopygium. The second segment is much longer than the third, and the third, fourth, and fifth segments are equal in length, the remaining segments shorter. Both the tergites and sternites are shining blackish in color and both with moderately abundant, fine, erect pile. In the females the abdomen is even longer and more attenuate, the terminal segments less telescoped and shortened and the female genitalia has on each side a vertical row of 7 or 8 stout, truncate, flattened spines.

The male terminalia from dorsal aspect, epandrium removed, show a very curious elongate structure, the very long tubular epiphallus reaches to the end of the dististyle and is deeply divided near the apex into 2 slender prongs. The dististyle is quite long, slender, curved on the inner and outer margins, convergent apically, the apex sharp. The basal apodeme is curious, very long, widening basally and basally spatulate. From the lateral aspect the dististyle forms a more or less shallow, lunate body curved forward both above and below, and quite thick on each end. The epiphallus is a curious structure, it makes a very strong, downward curve or bend, spoutlike. The basistyle and epandrium are both large. The basal apodeme is also quite prominent from the lateral aspect.

Material studied: Males and females of *Caenotus hospes* Melander, furnished by Dr. Melander from a large series he collected at Organ Pipe National Monument.

Immature stages: Unknown.

Ecology and behavior of adults: Melander (1950) recorded some of these flies coming to windows during the day, a few others attracted to lights; they were captured in April and May.

Distribution: Nearctic: *Caenotus canus* Melander, 1950; *hospes* Melander, 1950; *inornatus* Cole, 1923; *minutus* Cole, 1923.

Genus *Prorates* Melander

FIGURES 97A, 322, 326, 573, 700

Prorates Melander, Ent. News, vol. 17, p. 372, 1906. Type of genus: *Prorates claripennis* Melander, 1906, by monotypy. Described as Empididae.

Alloxytropus Bezzi, Bull. Soc. Roy. Ent. d'Egypte, vol. 8, p. 186, 1925c. Type of genus: *Alloxytropus anomalus* Bezzi, 1925, by original designation.

Melander (1927), p. 376, transfer to the Heterotropinae.

Efflatoun (1945), p. 98, key to 2 Egyptian species (as *Alloxytropus* Bezzi).

Small or very small flies which like *Heterotropus* Loew have colorless veins and generally pallid coloration, the legs especially are wholly pale yellow or whitish. Like *Heterotropus* Loew the eye is much enlarged in extent and sharply divided into a small lower division with minute facets and a more extensive upper division with much larger facets. Eyes in both genera markedly holoptic in males. Melander (1906) originally placed these flies in the family Empididae but in 1927 transferred them to the Bombyliidae.

In *Prorates* Melander the face is even more reduced, to a very small, narrow slitlike recess with small, short proboscis; from below the eyes curve under the head leaving only a small posterior triangle of occiput and the much reduced oral recess. Antennae smaller, and shorter than in *Heterotropus* Loew. In *Prorates* Melander the ambient vein is wanting, the costa ending at the third vein in contrast to *Heterotropus* Loew. Gen-

erally speaking the first and second branches of the medius originate from a common stem emitted from the discal cell, and this is true of the American species *claripennis* Melander, which he originally placed in the Empididae, and of the two Egyptian species, except that sometimes in the type-species, *anomalus* Bezzi, these two branches originate separately at the end of the discal cell. The genus is further unique in that the anal cell is closed with a very long stalk, the cubital vein having receded basalward. As Efflatoun (1945) remarks there is a general superficial resemblance to the Scenopinidae; it is just possible that the relationship is more than superficial.

These flies are known only from Egypt, New Mexico, and the Borrego Desert of southern California.

Length: 1.8 to 44 mm.; proboscis .5 to 1.8 mm.

Head, lateral aspect: The head is large, globular, with extraordinary development of the eyes. In the males only a small portion of the occiput is visible in the posterior ventral corner. The front is reduced to a very minute triangle, even smaller than the first antennal segment, and the face is reduced in space until it is not much larger than the front. The eyes extend forward and inward encroaching on space until even the oral recess is greatly narrowed, and the proboscis, which is relatively narrow, extends straight forward beneath the antennae for a short distance. The posterior margin of the eye is entire and the facets are sharply divided into a group of small, black facets on the lower third and much larger light-brown facets on the upper part. The palpus consists of a single, slender, elongate segment. The minute front is flat, lower than the surrounding eye margin, and micropubescent only. The antennae are relatively short; the first two segments are very short and the third segment more elongate and attenuate with a short, stump-like microsegment. The antennae are attached adjacent to one another but the third segment is thrust sharply outward at a right angle at the point of attachment. All of the segments are minutely micropubescent.

Head, anterior aspect: The head is distinctly wider than the thorax. In males the eyes meet for a long distance; the ocellar tubercle is raised, and comparatively large with large ocelli resting at the edge of the eye. The oral opening is narrow, but widens somewhat posteriorly, its depth equal only to that of the proboscis. The genae are quite narrow in front, gradually increasing in width behind.

Thorax: The thorax is relatively high, but only slightly convex over the middle and slopes from the transverse sutures gently back to the scutellum. Prothorax very short, the strongly developed eye tends to rest against both mesonotum, humerus, and prothorax. The mesonotum is opaque and has fine, grayish-white pollen, which under high magnification appears to consist of flat-appressed, scale-like hairs. In addition there are moderately abundant, fine, short, subappressed, slender bristles or bristly hairs. There are 2 distinct, stouter, and longer bristles on the notopleuron and a

pair of even longer slender yellow bristles on the margin of the scutellum, otherwise the scutellum and the pleuron are very similar to the mesonotum. The entire pleuron seems to lack pile except for the pollenlike micropubescent and a few isolated hairs on the lower mesopleuron and sternopleuron. Squamae large, thin, with a quite sparse fringe of scanty, stiff hairs of no great length. Halteres large, the knob large, thin-walled, elongate, and cup-shaped or rolled much as a rolled leaf.

Legs: The legs are quite slender, entirely pale, almost translucent in the dried specimen; the femora are very slightly thickened; the pile is everywhere minute, subappressed, rather scanty on the femora, more abundant on the tibiae. The anterior tibiae lack any longer setae that stand out from the abundant, appressed vestiture, but all of the femora have some suberect, fine setae that are a little longer than the remaining pile. Hind tibia similar to the anterior tibia. Pulvilli short, wide, and rounded apically, the sharp, slender claws are strongly bent and curved apically.

Wings: The wings are delicate, the veins colorless throughout, although the costa may be a little darker apically. The second submarginal cell is narrow and the basal fork narrow. There are 4 posterior cells, but the intercalary vein is absent, and the fourth and fifth longitudinal veins have coalesced for some distance away from the discal cell, so that the second posterior cell has a stalklike petiole. The anterior crossvein joins the discal cell near the outer third, and the stalk of the anal cell is even longer than in *Caenotus* Cole and is empidiform in character. The axillary lobe is large, the alula rounded but narrow, the ambient vein is entirely absent.

Abdomen: The abdomen is elongate, relatively narrow and attenuate as in some of the elongate species of *Aphobantus* Loew. I find 8 segments present. The pile is scanty, fine and erect and relatively short. The hypopygium is large, somewhat bulblike or clublike and rather conical though obtuse.

Material studied: A male of *Prorates claripennis* Melander.

Immature stages: Unknown.

Ecology and behavior of adults: Efflatoun (1945) notes that all these Heterotropini, and likewise the genus *Mariobezzia* Becker, are found only between the hours from 1 to 4, neither he nor his assistants seeing them at any other time. Melander (1950) collected his series in the early morning hours on the windows in his car where they had become trapped during the night; Efflatoun found they were sluggish, slow fliers hovering in the hottest hours of the day only.

Distribution: Nearctic: *Prorates claripennis* Melander, 1906.

Palearctic: *Prorates anomalus* (Bezzi), 1925 (as *Alloxytropus*); *bezzii* (Paramonov), 1929 (as *Alloxytropus*).

Genus *Apystomyia* Melander

FIGURES 85, 324, 599

Apystomyia Melander, Pan-Pacific Ent., vol. 26, p. 146, 1950b.Type of genus: *Apystomyia clinguis* Melander, 1950, by original designation.

Minute, slender, shiny-black flies with strongly humped mesonotum and with few, scattered, erect, bristly black hairs. The abdomen is elongate and attenuate and approximately twice as long as the thorax. The femora are slightly widened, especially the anterior pair. The wings are of milky-whitish appearance and also slightly iridescent when viewed obliquely. All of the veins are white, except the rather strongly developed costa and second vein.

Length: 3 mm.

Head, lateral aspect: As is so often true with the smaller Bombyliidae the head shrivels up until true proportions in dry material are virtually impossible to interpret. The head appears to be hemispherical, with a smooth, entire, posterior eye margin. The upper eye facets are enormously enlarged throughout most of the eye but without any clear dividing line between the minute facets below. In males the eyes are strongly holoptic for a considerable distance. The ocellar tubercle is triangular, raised above the eye margin by the full depth of the large ocelli, and lying between the ocelli there are 4 comparatively long, stiff, erect, black, bristly hairs. There are 2 other such hairs, even longer, which are placed posterodorsally on the frontal triangle above the antennae and at the confluence of the eyes. The face in the male paratype before me is sunken, probably due to a shriveling effect, however, it appears to be broadly triangular, much wider below. The antennae are large but with the first two segments very short and minute. The third segment is flattened, short oval, lamellate or leaflike, micropubescent, and bears a curious, slender, very short, cylindrical style or microsegment which has minute bristles. The sides of the facial triangle have a row of long, erect, scattered, bristly hairs on each side that are similar to those of the front and vertex. The proboscis is very short and consists of a mere pad or labella-like stub at the base of the head and presumably nonfunctional. On each side of the labellum is a minute, translucent, yellowish white palpus. Lateral margin of the occiput with scattered, erect, bristly hairs.

Head, anterior aspect: From the frontal view the eyes are widely holoptic leaving a comparatively small, approximately equilateral triangle which constitutes the frontal triangle above the antennae. The line of contiguity extends from the large ocelli almost to the antennae, and there are no notches present. The upper eye facets are exceptionally enlarged, but, because the eyes are deeply shrunken inward on both sides in my specimen, I cannot tell if there was a horizontal dividing line present. Melander, however, notes that the lower facets of the eye are abruptly minute. Below the antennae the

oral recess or clypeal recess is very broad and large, obliterating the face that bears rather numerous long, erect, black hairs which are at no place dense. There is a blunt stump of a proboscis.

Thorax: Rather strongly humped, less so than in *Mythicomomyia* Melander. It is very highly polished black in color, with perhaps a dozen erect, scattered, long, stiff bristles or bristly black hairs lying on each side of the anterior half of the mesonotum. There are 3 or 4 other similar bristly hairs on the posterior half of the mesonotum; among them is a longer element on the postalar callosity. The margin of the flat and rather pubescent scutellum has a conspicuous row of erect, long, black bristles or bristly hairs. The metanotum is large, shiny, and without pile. The entire pleuron appears to lack pile or pubescence of any kind.

Legs: Brownish black. The anterior femur has a dorsal row, a ventral row, and a more conspicuous lateral row of long, black bristly hairs. There are about 10 such hairs placed ventrally, about 7 placed dorsally on the outer half and about 10 placed laterally on the outer two-thirds of this femur. Anterior tibia with a dorsal row containing 6 long, slender, black bristles and near the apex 3 or 4 shorter ones. Middle femur with similar bristles and its tibia with 2 or 3 rows of somewhat shorter, but stouter black bristles; there are 7 or 8 bristles in each row. These tibial bristles become more numerous at the middle of the tibia and beyond. The hind femur has a ventral and a lateral row with slender, whitish, bristly hairs. Its tibia has 1 or 2 rows of weaker, shorter, whitish, bristly hairs. Claws slender and sharp; the pulvilli are well developed. Upon the hind legs the basal half of the first tarsal segment and all of the third and fourth segments are whitish due to the presence of a dense, white micropubescence; and some of the bristles are white. Middle tibia with a curious, black, thick, subapical process or downward projection, composed possibly of fused bristles; the apex of middle basitarsus with a curious apical offset swelling in the direction of the tibial process, and from which the next tarsal segment arises.

Wings: Weak, broad at the base, the axillary lobe especially deep and broadly rounded posterior basally. The alula is present but narrow and in shape gently rounded, both at base and apex, hence with a shallow curvature. The wings have a strong milky whitish cast yet are iridescent from an oblique view. All of the veins are whitish, except the costa and the second vein, both of which are very stout. There are coarse, sharp, oblique, stout setae on the costa. The anterior crossvein is close to the basal third of the very long, slender discal cell. There are 2 submarginal cells but the third vein is almost straight or plane from its origin to the apex of the wing. The anterior branch arises rectangularly, quickly turns toward the apex of the wing, curving over slightly. While there are 4 posterior cells, the discal cell is not quite as long as the cell itself. Second submarginal cell short; its shape hemicircular. The second basal cell is very long, slightly but progressively

widened, it is much longer than the first basal cell, and twice as long as the third basal cell. Its length from its base is fully equal the remaining length of the fourth vein to the wing apex.

The costal cell is much widened toward the base, the costa ends at the apex of the wing so there is no ambient vein. Posterior margin of the wing with a distinct fringe and with an especially long fringe in the bend and basal margin of the axillary cell. The anal cell is closed, and the stalk or petiole is almost as long as the last section of the third vein beyond its fork.

Abdomen: Tapered and quite narrow apically. The hypopygium is a little enlarged and clublike. It is dully shining black and has a few, fine, erect, scattered white hairs on all the tergites especially laterally. There is a tuft of scattered, sparse, scanty, long, white pile, laterally on the sides of the first tergite. On the hypopygium there are some quite short, scattered, white hairs.

Because this is a very peculiar fly and because of its relationship within the Bombyliidae, I quote Melander's brief description to supplement my own:

Eyes of male contiguous from ocelli almost to antennae, not notched, the facets of upper two-thirds coarse, lower facets abruptly minute; front of female very broad above; occiput quite flat; ocelli of male large, on the elevated vertical triangle; mouth opening broad and large, obliterating the face, the cheeks wide, eyes distantly separated below; antennae inserted low on head, basal joints minute, third joint rotund and compressed, microscopically pubescent, the apical style cylindrical, blunt, about one-third as long as the third joint; mouth parts vestigial, fleshy, not projecting. Thorax glistening jet black, with long coarse hairs, scutellar margin setose; pleurae bare. Abdomen

slender, tapering, pilose in male, not tomentose, pygidium minute, globular, with two small erect spatulate dorsal palps enclosed by a pair of almost triangular lateral valves tipped with a few setulae, ventral piece small. Legs with coarse hairs, almost setose on femora and tibiae, without tomentum, pulvilli present. Wings very delicate, costa continuing to fourth vein, first vein chitinized, other veins of male thin and translucent, anal lobe very large, alulae moderate, third vein forked near tip of wing, fourth vein forked, the petiole of second posterior cell about as long as posterior crossvein, discal cell narrow, elongate, anterior crossvein at basal third, petiole of anal cell about as long as the arched anal crossvein; calypteres with nearly straight edge, heavily fringed.

Material available for study: A paratype male of the unique type-species furnished through the kindness of Dr. W. W. Wirth and Dr. Karl Krombein of the National Museum of Natural History makes it possible to include this genus within this monograph. Several years ago Dr. Melander, during a personal visit at his home, had offered me a specimen but was unable to locate his series at the time.

Immature stages: Unknown.

Ecology and behavior of adults: Dr. Melander collected his material sweeping vegetation at Wrightwood, California, on the north of San Gabriel Mountains, May 24. He obtained them by sweeping vegetation along a small stream that later entered Sheep Creek Canyon. He also obtained them on Sugarloaf Mt. in the San Bernardino Mts., May to July, and also on Mt. San Jacinto on May 7.

Distribution: Nearctic: *Apystomyia elinguis* Melander, 1950.

Subfamily Toxophorinae Schiner, 1868

This small subfamily of peculiar flies is noted for its humpbacked, robust or sometimes elongate-cylindroid appearance and for the strong bristles upon the mesothorax and prothorax and the legs. These macrochaetae are not only long as a general rule, but in *Toxophora* Meigen they are particularly strongly curved; they are stout basally, sharp apically. All the genera in the subfamily are notable for the unusually prominent, although variable, prothorax, beset with either macrochaetae or spikelike bristles. The wings are variable: small in *Toxophora* Meigen, larger and more elongate in remaining genera. *Lepidophora* Westwood has many scales upon the anterior half of the wing; *Cyrtomyia* Bigot has scales on the basal half. In some genera the wings are mottled or spotted about the crossveins and furcations. The general coloration of the flies is black,

relieved in *Toxophora* Meigen by pale pile and dense, matted, scalelike pile placed in bands or spots upon the abdomen. Some species are metallic.

The antennae are elongate, the third segment is sometimes very thin, acutely pointed, as in *Toxophora* Meigen, or shorter in other groups. The first segment is quite elongate, the second usually lengthened but shorter than the first. In *Lepidophora* Westwood the antennae are very long and the first two segments show numerous, conspicuous, largely erect scales, and similar scales adorn the terminal segments of the abdomen.

The femora of *Toxophora* Meigen are swollen and thickened, especially the hind pair, and they are likewise covered with matted scales. There is apt to be a long, troughlike hollow on the ventral sides of the first four femora in this genus in both sexes. The femora in

Toxophorinae



TEXT-FIGURE 32.—Pattern of the approximate world distribution of the species of the subfamily Toxophorinae.

this genus frequently, if not generally, lack bristles; whereas, other genera in the subfamily have spinous bristles below in both sexes upon at least the hind femur.

A close study of these flies reveals several peculiar features. In the first place the occiput is not hollowed and cupulate as in Cylleninae or in the Lomatinae, and it is not bilobate above behind the vertex as in those groups. Rather, I feel that these flies represent aberrant offshoots of early Bombyliina stock, and so I place them in the Division Homoeophthalmae; the posterior eye contour is virtually plane.

In *Toxophora* Meigen the anal cell is closed; there are usually 2, but sometimes 3, submarginal cells; in the subgenus *Eniconeura* Macquart the second branch of the medius is partially atrophied. The wings are spotted in *Marmasoma* White, a more elongate fly with tapered abdomen.

Toxophora Meigen parasitizes vespids; it has been reared by Krombein from odynid-type wasps where it fed on pupae or prepupae and occurs also in the nests of eumenids feeding on either the wasp larvae or the caterpillars they store. Krombein (1967) notes that *Lepidophora* Westwood larvae feed on vespid larvae, and often upon the caterpillars they store and in one instance spiders stored in the nest of a species of *Trypar-*

gilum; see discussion under life histories.

Toxophora Meigen is the only genus in the subfamily that is of worldwide distribution. Has the strong bee-like appearance of these flies been a factor in their successful persistence?

The genera within this subfamily are certainly disparate. Hence, I place *Toxophora* Meigen in the tribe Toxophorini and the remaining genera within the tribe Lepidophorini, distinguished by the subglobular head, very swollen occiput and the spikelike occipital bristles.

The subfamily Toxophorinae is characterized by an oval figure in which the dististyli are triangular from dorsal aspect. From the lateral aspect it is very deeply incised dorsally into two subequal sections, in fact, almost cut in half. *Toxophora* Meigen is much more distinct from *Lepidophora* Westwood which is nearly allied to *Cyrtomyia* Bigot. These latter two show a closer relationship, both in the very short, oval form, the large, conical epiphalli, and the dististyli. For this reason I place them in a separate tribe, also pupal characters suggest that they should be separated. After preparation of this work was completed, I revised my views on this subfamily on the basis of pupal characters. I now believe all four genera of the Lepidophorini should be placed as a separate tribe within the Bombyliinae.

KEY TO THE GENERA OF THE TOXOPHORINAE

1. Occiput with dense, rather short, erect pile of no great length. Stout, rather flattened and short, robust flies with strongly arched mesonotum and decumbent head and abdomen. Antennae elongate, especially the first segment; second segment of male antennae with a conspicuous elongate, medial patch of brilliant, silver, microscopic pollenlike microsetae. Third segment slender, elongate, flattened apically, with long attenuate, sharp-pointed style. Only 3 posterior cells. Propleuron and pronotum unusually prominent and bearing, very long, stout, curved macrochaetae, continued along front margin of mesonotum. 2

Head subglobular, with extensive occiput, not bilobate and not cupulate; at most with faint postvertical crease. Occiput with numerous erect, long, spikelike bristles. Pronotum and anterior mesonotum to a lesser extent with stiff bristly hairs but not with stout, long, curved, scimitar-like macrochaetae. Always with 4 posterior cells; usually with 2 submarginal cells 3

2. Three posterior and 3 submarginal cells.

Toxophora Meigen

Three posterior and 2 submarginal cells.

Toxophora (*Toxomyia*, new subgenus)

Three submarginal cells and second branch of medius only partially atrophied. *Toxophora* (*Eniconeura*) Macquart

3. Antennae unusually elongate, the first two segments both elongate and both covered with dense, lateral fringe of long, broad, erect, conspicuous scales; anterior half of wing, except apex, with numerous smaller scales. Tergites of abdomen laterally with scales, growing longer, wider, tuftlike, and conspicuous on the apex of the abdomen. Strongly humpbacked flies with decumbent head and abdomen. Prothorax very prominent.

Lepidophora Westwood

Not such flies. Second antennal segment short and beadlike; prothorax much shorter, its bristles much weaker. Venation and head and antennae very similar to *Thevenimyia* Bigot, but anterior branch of third vein ends above the wing apex and these flies are decumbent. Palpus varies from 2- to 3-segmented 4

4. Wings with scales on basal half. Stout bodied, robust flies, strongly decumbent *Cyrtomyia* Bigot

Wings without scales. More slender, less strongly decumbent flies *Marmasoma* White

Genus *Toxophora* Meigen

FIGURES 91, 92, 316, 317, 558, 577, 865, 866

Toxophora Meigen, Mag. Insektenkunde, vol. 2, p. 270, 1803. No species. Type of genus: *Asilus maculata* Rossi, 1790, designated by Meigen, p. 273, 1804; one species.

Eniconeura Macquart, Diptères exotiques, vol. 2, pt. 1, p. 110, 1840. Type of subgenus: *Eniconeura fuscipennis* Macquart, 1840, by monotypy.

Heniconeura Verrall in Scudder, Nomenclator Zoologicus, p. 159, emendation, 1882.

Toxomyia, new subgenus; type-species: *Toxophora maxima* Coquillett, 1886b.

Coquillett (1891a), p. 199, key to 6 Nearctic species.

Bezzi (1924), pp. 129-130, key to 8 Ethiopian species.

Paramonov (1925), p. 43, key to Palaearctic species.

Engel (1933), p. 82, key to 5 Palaearctic species.

Maughan (1935), p. 71, key to 2 U.S. species.

Hesse (1938), pp. 1032-1036, key to 7 male and 7 female species from South Africa.

Efflatoun (1945), pp. 186-187, key to 3 species from Egypt.

Bowden (1964), p. 53, key to 3 species from Ghana.

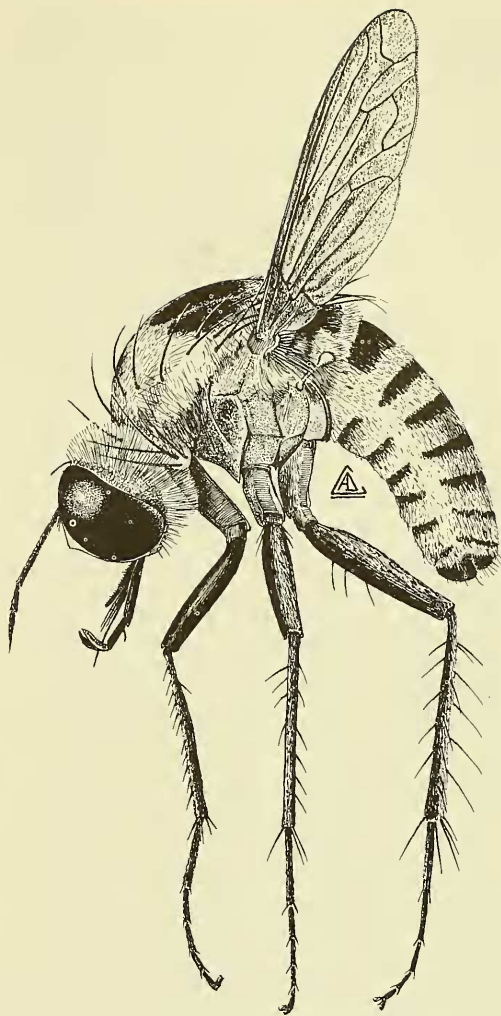
Strange, stout, robust flies of small to medium size, which are readily recognized by the characteristic humpbacked form and the long, basally stout, apically pointed, much curved bristles upon the thorax. The legs also have spinelike bristles. They are black insects with bands and spots of matted pale-colored pile on the strongly decumbent abdomen; a few tropical species are metallic green or violaceous. The head is also decumbent and the antennae long with the third segment attenuate and sharp at apex; most males have a brilliant patch of silver pollen on the inner side of the second segment.

The nearest relative is *Marmasoma* White, a Tasmanian and Western Australian genus; it differs from *Toxophora* in the shorter, nonscaly antennae, the less conspicuously drooping head and abdomen, the open anal cell, and the long full row of bristles on each side of the front.

Toxophora species are distributed throughout all world regions but appear to be most abundant in the Southwestern United States and western Mediterranean.

Length: 6 to 12 mm., including antennae; wing, 4 to 7.5 mm.

Head, lateral aspect: The head is subglobular, while the eye is only hemispherical and constitutes the greater part of the head anteriorly. The occiput is more or less swollen posteriorly both in males and females and heightened by dense, spikelike, long pile, or bristles extending backward. The occiput is most extensive centrally, with small, shallow medial depression where the head is joined to the thorax, and from this point it is quite convex and slopes strongly out to the eye margin. Outer part of the occiput covered with dense, appressed scales reaching to the eye margin. Posterior part with dense, erect or obliquely erect fringe of long, somewhat flattened, spikelike bristles. The front in males is reduced to a minute triangle above the antennae bearing a dense, matted tuft of flattened, bristly hairs diverging on each side of the antennae, and in females slightly raised above the eye margin with shallow, central fovea or depression, and with the triangular middle area again with appressed, flattened, bristly pile. The eye is exceptionally large, occupying the greater part of the head, and shows a certain amount of overgrowth posterolaterally, thus reducing the occiput and leaving the greatest eye width at some distance away from the posterior margin. Posterior eye margin laterally not quite plane on the upper half, strongly rounded below; the upper facets in the male are strongly enlarged. From the lateral aspect the face is always quite short, varying a little in extent, but it is relatively long and extensive below the antennae because the large oragenal cup ends some distance away from the antennae. The genae, how-



TEXT-FIGURE 33.—Habitus, *Toxophora leucopyga* Wiedemann.

ever, are narrow and rimlike. Face and genae with pollen and minute pubescence only.

The proboscis ranges from 1 to $1\frac{1}{2}$ times the length of the head; it is thrust forward, compressed laterally, with long, narrow, attenuate labellum, which bears laterally many short, erect, spiculate setae. The palpus is quite long and slender and is usually half as long as the proboscis, attenuate, and slightly curved upward; it has a scanty fringe of moderately long, bristly hairs on the outer margin and often shorter bristly hairs on

the dorsal and ventral surfaces. The antennae are attached near the top of the head and are extraordinarily long and slender, especially the first segment. The first segment is cylindrical, nearly or quite as long as the head and bears broad, dense scales on all sides. They are, however, sometimes absent below. In addition, there are a few, subappressed, short, black, bristly hairs medially and some setae at the apex. Third segment a little expanded distally with numerous, appressed, short black bristles; in males the medial surface of this segment shows a long, widening patch of silvery pollen extending almost the full length of the segment; and in females there may be a small patch of similar pollen near the apex. The second segment is about one-third as long as the first segment or sometimes a little longer proportionately. The third segment is no wider than the second but is strongly attenuate apically, ending in a long, spurlike style, which is sometimes colored differently and longer in the male than in the female; it is very sharp-pointed, the whole third segment, style excepted, is only a little longer than the second segment.

Head, anterior aspect: The head is almost but not quite as wide as the thorax. It appears to be set in a drooping position partly because of the prominent prothorax and the very high thorax with convex mesonotum. The eyes are strongly holoptic in males, tightly apposed for at least 3 times the length of the front. The ocellar tubercle is comparatively low, the ocelli occupying a somewhat obtuse triangle or sometimes an equilateral triangle and characteristically with a pair of extremely stout, curved, sharp-pointed, spikelike bristles, arising behind the ocelli and directed forward. The eyes in the female are rather widely separated, the front narrowed slightly above, the vertex separated by more than twice the width of the ocellar tubercle. The antennae are adjacent, the head is widest below. The width of the face is about one-fifth the maximum eye width and the oragenal cup peculiar because it appears to have a double wall. The wall consists of an inner portion encircling the oral cavity above and actually ending in the face, since the upper half of the oral recess slants strongly upward and forward until it is level with the facial prominence. This inner wall sinks downward below until it is rather deep within the recess and is quite distinct from a low, vertical rim arising at the bottom of the oral cavity and which extends at least halfway up the oral cavity, leaving the gena narrow but clearly demarcated along the eye margin. Rather near the top of the oragenal recess, between these two walls, there appears to be a shallow tentorial fissure.

Thorax: The thorax is short and compact. The mesonotum is convex although not especially high. The pronotum is unusually prominent and is characteristically large and well developed in this subfamily. The head and especially the abdomen are strongly decumbent in their attachment to the thorax. The mesonotum is almost always strongly denuded in captured individuals but there is generally undisturbed pile along the lateral and anterior margins and narrowly in front of the

scutellum and on the brief declivitous portion of the mesonotum. Occasional individuals can be found in which the mesonotal pile is nearly intact. It may be continuous or vittate and consists of dense, lanceolate, flat-appressed scales extending matlike in many directions. In addition, there is much dense, much longer, pointed, delicate, scalelike pile in matted or curled, more or less erect tufts on the anterior and lateral margins, continuing widely over onto almost the whole of the mesopleuron and the whole of the propleuron and pronotum. Along the sides of the mesonotum above the wing, on the postalar callosity and in front of the scutellum and on the margin of the scutellum itself, there is a border of flat-appressed scales intermediate in length between those of the mesonotum and the longer pile on the anterior part of the thorax. In addition, nearly all species of *Toxophora* Meigen have on the mesonotum minute, flat-appressed, black scales which are largely confined to the posterior half of the mesonotum but may form vittate stripes extending forward. These appressed, black scales continue onto the scutellar disc where they are conspicuous and usually larger.

Characteristically, the pronotum and mesonotum have a number of extraordinarily long and basally stout, apically sharp, curved, conspicuous macrochaetae. They form a border on the pronotum of 3 to 7 pairs so long that they curve backward like scimitars over the mesonotum; usually black, sometimes a few are yellow. In addition, there is a row across the anterior part of the mesonotum of similarly long, curved macrochaetae consisting of 2 or 3 pairs. Another is immediately behind the humerus, 3 or 4 between the humerus and the wing base, and a small cluster on the posterior notopleuron, sometimes reduced to as few as 2 or 3; several macrochaetae are above the wing itself; 1 to 3 upon the postalar callosity and several pairs on the margin of the scutellum which are apt to be of varying size and stoutness. There may be a prescutellar pair widely separated, and the outermost pair on the scutellar margin is apt to be much bigger than the others. Upper border of mesopleuron with a horizontal row of several similar macrochaetae. The propleuron is pilose. There is a patch of appressed pile posterodorsally on the sternopleuron, but the pteropleuron, metanotum, hypopleuron, are without pile; except on the latter, a patch of pile is behind the spiracle and below the halteres. Halteral knob with a patch of scales behind in some species. Halteres short but the knob large. The squama is of variable length, sometimes very short, sometimes longer but with more or less plane and thickened margin, always bearing a very conspicuous, marginal fringe of dense, quite long bristles, umbrella-like over the haltere. At the base of the squama medially there is a flattened element that apparently corresponds to the strigula of *Systropus* Wiedemann.

The scutellum of *Toxophora* Meigen is large, wide, and rather flattened becoming thinned and descending backward as a ledge over the whole of the short metanotum. Lateral wall of the metapleuron is thin, extend-

ing straight outward behind the haltere. Metasternum short and not sclerotized.

Legs: The legs are unusually stout, especially the femora which are more or less thickened throughout, and the hind femur is the stoutest of the three pairs; it is slightly arched below, more so above. The legs are relatively short, the middle pair a little longer than the front pair and the hind pair a little longer than the middle pair. The femora lack spines or bristles, except rarely the hind femur has a short row ventrally on the basal half. All the femora are densely covered with large, broad, rather short, shinglelike scales, quite flat-appressed, ranging from white, yellow, metallic, or blackish in color. Tibiae with conspicuous, stout, sharp, black bristles. The anterior tibia has a double dorsal row of bristles; the anterior row consists of 6 to 9 bristles, the posterodorsal row has 5 to 8 bristles. There is also a posterior row of 3 to 5 bristles and sometimes additional ventral bristles. Middle tibia with similar and longer bristles, which, however, are more irregular in size and distribution. The hind tibia is stouter than the others and its bristles more erect, large and spike-like. At the base a group of 3 or 4 are placed together transversely, and there are posterodorsal and anterodorsal rows, each consisting of about 4 or 5 bristles. Apex of each tibia with very long, spikelike bristles especially ventrally. Surface of all tibiae covered with loose, shinglelike scales. Tarsi short, slender, especially on the terminal segments, with short setae below and a dense covering of fine, long, flat-appressed setae. Claws long, stout, comparatively blunt and much curved at the apex and the pulvilli long. The last tarsal segments in some species, in males especially, have on each side ventrally a comb of very stout bristles. Lower surface of anterior femur sunken or hollowed and sometimes rugose.

Wings: Wings either hyaline, tinted with brown or yellow, or rarely mottled or spotted. They are relatively short, narrowed at the base. There are 2 or 3 submarginal cells; that part of the vein constituting the second part of the radius is sometimes lost. The anterior branch of the third vein is rectangular; at times it simulates a crossvein; in any case, it is sharply bent outward. The anterior crossvein enters the discal cell at the middle or sometimes at the outer curve; the second branch of the medius may be atrophied completely or partially; hence there are only 3 posterior cells. The anal vein is always closed and petiolate, the cubitus making a strong arch distally. Axillary lobe narrow and the alula of about the same width as the base of the axillary lobe; the ambient vein extends to the end of the first anal cell. There is a thickening of the radial sector. Whole wing villose.

Abdomen: The abdomen is stout, strongly convex, and at the base as wide or even wider than the mesonotum. It may be a little longer and sometimes no longer than the thorax, and it is gradually narrowed and tapered to the end of the first segment. Eight tergites are visible in both sexes and they bear dense, flat-

appressed, rather broad, short scales on the basal part of each tergite, except sometimes the last one, and these broad blackish, dark-colored scales often form continuous or paired fascia or a series of spots. The posterior margins and the lateral margins narrowly or widely are covered with matted scales of greater length and in most species yellow or white in color. Sternites generally covered with pale scales throughout and in the middle of each sternite with a curious little tuft of 4 quite fine, somewhat rather long, erect hairs. Female terminalia compressed and without spines. Male terminalia sometimes protrusive and large; in other species completely recessed.

Because of the large number of species that Dr. A. J. Hesse was able to study and summarize, I quote his work on the hypopygium of the males:

Hypopygium of males as in the case of *Systropus*, appears to act in conjunction with the last abdominal segment and the basal part of the hypopygium is constantly ventral in position, the opposing sternite being dorsal or tergal in position. This last sternite is attached to each side of basal part of hypopygium by a stoutish, chitinous process. This process may be roughly club-shaped, thickened at middle and bifid apically or blade-like. It sometimes has a tuft of longish, bristly hairs or it may be smooth. The last sternite ends apically on each side in a terminal plate, probably representing modified last abdominal elements as in other genera. These plates are usually quadrangular or sub-quadrangular, but may also be bilobed, the outer lobe with a comb or crown of short spines. The basal part of the aedeagus is often produced apically into a comb of flattened spines or into a medial process or bilobed process, or it may be without any comb or process. Lodged apically in the basal part is a distinct apical joint (segment) on each side. This apical joint (segment) may be flanked on the outer side by another process, which has shortish, stoutish, spine-like hairs directed brush-like towards the apical joint (segment). The aedeagal complex is joined on to the basal part beyond the middle on each side by a trace-like or strap-like ramus, which usually forms a flattened process or plate, extending from sides of basal part. This plate really consists of the base of the ramus doubled upon itself, the basal part of which joins on to the process on each side of last sternite. The aedeagal complex consists of a true apical aedeagal part, usually curved towards the basal parts.

The male terminalia from dorsal aspect, epandrium removed, show an oval structure with curious, short, triangular dististyli. The basal ejaculatory apodeme is short. There appears to be an accessory anterior apodeme in addition to the more basal lateral apodeme. From the lateral aspect the epiphallus and ejaculatory process are situated quite high near the top of the epandrium. The dististyli are short, stubby, pointed at the apex but curved backward, and the basistylus has a ventral, apical notch or incision.

Material studied: Numerous Nearctic and Neotropical species.

Immature stages: The larvae are parasitic in wasp nests. See discussion under life histories.

Ecology and behavior of adults: The adults frequent plants of the family Compositae of many genera and species.

Distribution: Nearctic: *Toxophora americana* Guérin-Méneville, with fig. only, 1835; *amphitea* Walker, 1849; *leucopyga* Wiedemann, 1828 [= *fulva* Gray,

1832]; *maxima* Coquillett, 1886; *pellucida* Coquillett, 1886; *vasta* Coquillett, 1891; *virgata* Osten Sacken, 1877.

Neotropical: *Toxophora amacula* Ségué, 1930; *aurea* Macquart, 1848; *aurifera* Rondani in Truqui, 1848 [= *dryitis* Ségué, 1930, = *verona* Curran, 1934]; *cuprea* (Fabricius), 1787 (as *Bombylius*); *lepidocera* d'Andretta & Carrera, 1950 (subg. *Eniconeura*); *leucon* Ségué, 1930 (subg. *Eniconeura*); *pallida* d'Andretta & Carrera, 1950; *travassosi* d'Andretta & Carrera, 1950 (subg. *Eniconeura*); *tristis* Ségué, 1930 (subg. *Eniconeura*); *varipennis* Williston, 1901; *zikani* d'Andretta & Carrera, 1950 (subg. *Eniconeura*).

Palearctic: *Toxophora aegyptiaca* Efllatoun, 1945; *bezzi* Paramonov, 1933; *deserta* Paramonov, 1933, *deserta tadjikorum*, 1953; *epargyra* Hermann, 1907; *fuscipennis* (Macquart), 1840 (subg. *Eniconeura*); *lebedevi* Paramonov, 1925; *leyladea* Efllatoun, 1945; *maculata* (Rossi), 1790 (as *Asilus*), *maculata completa* Paramonov, 1933 [= *fusciculata* Villeneuve, 1789, = *maculata* Meigen, 1904]; *psammophila* Paramonov, 1935; *shelkornikovi* Paramonov, 1953; *turkestanica* Paramonov, 1933, *turkestanica angusta* Paramonov, 1933; *zilpa* Walker, 1849.

Ethiopian: *Toxophora albivittata* Bowden, 1964; *australia* Hesse, 1938; *carelli* Guerín, 1831; *chopardi* Ségué, 1941; *coeruleiventris* Karsch, 1887; *crocisops* Hesse, 1938; *cyanolepida* Hesse, 1938; *diptera* Speiser, 1910; *epargyroides* Hesse, 1938; *maculipennis* Karsch, 1886; *obliquisquamosa* Hesse, 1938; *quadriculata* Hesse, 1963; *punctipennis* Bezzi, 1921; *seyrigi* Ségué, 1934; *trivittata* Bezzi, 1908; *vitripennis* Bezzi.*

Oriental: *Toxophora javana* Wiedemann, 1821.

Australian: *Toxophora compta* Roberts, 1929.

Genus *Lepidophora* Westwood

FIGURES 90, 318, 457, 540, 869, 870, 871

Lepidophora Westwood, London and Edinburgh Philos. Mag. and Journ. Sci., vol. 6, p. 447, 1835. Type of genus: *Toxophora lepidocera* Wiedemann, 1828, by monotypy, as *Ploas aegeriformis* Gray, 1832.

Painter (1925), p. 120, key to 4 species.

Paramonov (1949), pp. 632-633, key to 7 New World species.

Painter (1962), pp. 50-52, comments on several species.

Quaint and unique flies of medium to large size that are readily recognized by the strongly humped and arched thorax, the decumbent head and decumbent abdomen, also the presence of large, long, broad, black and partly yellow or white scales upon the sides and apex of abdomen, and abundantly on the elongate antennae. The wings are usually smoky, or subhyaline with the veins darker. The second vein and the anterior branch of the third vein make a strong, rounded rectangular bend forward near the apex of the wing. All cells

widely open, except the anal cell, which is narrowed; alula well developed; anterior crossvein lies at the middle of the long, narrow discal cell. There are small dark scales on the basal half of the anterior half of the wing and an odd tuft of white or yellow scales at the base of the weak basal comb. The prothorax is strongly developed; it has a spikelike, transverse row of long, stout bristles followed behind in the middle with a large dense patch of erect scales. Head subglobose, the occiput much swollen, especially above, and with numerous spikelike bristles but not bilobate. All femora and tibia with strong, spikelike bristles. Proboscis about $1\frac{1}{2}$ times as long as head; palpus elongate. Oral recess very large, the gena quite narrow but with a row of bristles.

Lepidophora Westwood is a small Nearctic and Neotropical genus ranging into Brazil. Paramonov (1949) described a species from Central Africa, which I have not seen, transferred by François to *Palintonus*, new genus.

Length: Thorax 7 mm., abdomen 6 mm., head 2 mm., antenna 4 to 5 mm., wing 7 mm. to 11 mm.

Head, lateral aspect: The head is globular; occiput unusually tumid but rounded and gradually sloping out to the eye margin. The face projects a short distance near the top of the head; the pile of the face consists of long, wide, erect scales thrust outward near the anterior border of the face in a complete row beneath the antennae. The scales become shorter laterally on the upper corners of the oraginal cup and give way to short, erect bristles below, which arise from the gena. The pile of the occiput consists of numerous, broad, yellow, erect scales, those arising medially are longer, those near the eye margin shorter and more or less appressed to the occiput. Below these scales change to blackish and in other species they may be gray or white, but on the dorsal half of the occiput arising centrally and medially there are numerous, sharp, black, long, erect, spikelike bristles that scarcely rise above the vertex. Pile at the bottom of the occiput and between the eyes consists of long, fine, scanty, scattered hairs. The eye is quite hemispherical and large, the posterior margin entire, almost plane. In males the upper facets are not enlarged. The proboscis is elongate and compressed laterally and from this aspect rather stout. The labellum is similar and one-third the total length of the proboscis. It bears microscopic setae and the whole proboscis is less than $1\frac{1}{2}$ times as long as the head. Palpus large, robust, and rather elongate, extending beyond the oral cavity.

Antennae attached quite at the top of the head, they are remarkably elongate, from $1\frac{1}{2}$ to 2 times as long as the entire head, slender, the first segment extraordinarily long, nearly 3 times as long as the long second segment and the second segment slender, and 5 or 6 times as long as wide; its width is deceptive because of the thick covering of scales. Third segment small, quite slender, knobbed at the base and attenuate at the base and with a medial groove. The first and second segments of the antenna both bear dense, short, suberect, blackish or gray scales dorsally and still longer, equally

* Bezzi (1924), p. 20, lists a *Toxophora vitripennis* Bezzi. I have been unable to find this species in print, or listed in *Zoological Record*; it may be a nomen nudum.

numerous, oblique, or subappressed scales ventrally. Those on the second segment tend to be thrust outward in a lateral plane. The third segment bears some short, strong setae laterally on the basal half.

Head, anterior aspect: The head is almost circular, being very little wider than high. The occipital scales and bristles both appear from the front and the head is much narrower than the thorax. Eyes of male narrowly separated by the width of the posterior ocelli at their outer margins. The front where the eyes approach is quite short, this area scarcely longer than wide and pollinose only and likewise flattened. The more extensive area of the front anteriorly before the antennae is somewhat raised and covered with short, broad scales and longer, scattered, slender bristles. Scales often with patches of different color. The antennae are narrowly separated by about half the thickness of the first segment. The ocellar tubercle is quite low, not all protuberant; it is also small and the small ocelli lie in an equilateral triangle from the center of which arise 7 or 8 moderately long, fine, bristly hairs. The oral opening is quite large, oval, and unusually deep anteriorly as well as posteriorly. Its margin is almost knife-thin, except at the extreme rear, where it is a little thickened on each side. The genae are linear and very narrow, the tentorial fissure is completely occluded from above. The postoccipt cannot be seen without removal of head.

Thorax: The thorax is rather long and narrow, laterally compressed, strongly compressed anteriorly and posteriorly with both head and abdomen strongly decumbent. The prothorax is extensive and long, convex across the middle, thus creased behind and sloping in front. The pronotum bears long, slender, erect scales, black in the middle, yellow laterally, in some species gray or white, and often intermixed are some coarse hairs of the same color, the hair becoming denser and more in evidence laterally. Anterior margin of the pronotum with a row of long, slender, black bristles, a vertical row laterally of 7 bristles. The elongate, convex humerus bears 10 or 15 slender, black bristles. Mesonotum black with opaque sepia pollen and rather densely covered with short, slender, curved scales, yellow to white to gray in different species. These scales are semiappressed, become longer opposite the wing and on the postalar callosity and on the margin of the scutellum. Laterally it gives way to coarse pile on the corners of the scutellum. The notopleuron bears 5 quite long, rather slender, black bristles. There are other finer, but shorter, bristles. The postalar callosity has 3 long bristles, the scutellar margin has 5 or 6 pairs of black bristles on each side, which are long and some additional slender, black hairs. Vertical outer sides of the postalar callosity without pile, except for dorsal pile that turns over and except, for an anterodorsal, peculiar tuft of long, fine, yellow hairs.

Whole mesopleuron covered with long, coarse, yellow hair slightly appressed backward, some of the hairs becoming flat apically. Pteropleuron with a few hairs anteriorly; hypopleuron with an extensive tuft of hair

long and fine on its anterior half, a curious tuft of short, dense hair immediately beneath the haltere and behind the spiracle adjacent to it. Spiracle with a setate rim. Metapleuron bare with a flat, shelllike lobe. Squamal fringe moderately thick but quite fine.

Legs: The femora are stout, the anterior pair rather short, the tibiae and tarsi slender, and the last 4 rather long. Anterior tibiae with stout spicules in 2 rows. There are 6 posterodorsally, 3 posteriorly, only minute setae elsewhere. On the midtibia the spicules are stout and long, in 4 rows, 5 very stout ones anterodorsally, 4 shorter ones posterodorsally, 4 stout ones posteroventrally and 3 or 4 anteroventrally. Hind tibia likewise with 4 rows of stout spicules, 4 or 5 in each row. The femora are not enlarged basally, all 3 pairs bear some stout, spinous bristles. The anterior femur bears a circlet of spines near the apex, midfemur with 4 anteriorly, hind femur with 6 ventrally, and 5 others circling the femur near the apex. Pile of the legs composed of dense, short, wide, flat appressed scales, a few fine, short, erect hairs and sometimes erect, long, slender scales toward the apex. Dorsal scales tend to be dark, ventral scales tend to be pale.

Wings: The wing is long and slender, tinged with brown or gray. Margin of the costa in males with nodulous, spinous tubercles. All the posterior cells widely open, the anal cell narrowly open. Anterior branch of the third vein makes a zigzag bend and at the corner of its first bend often has a backward spur. The second vein makes a rectangular bend toward the costa and often has an outward spur at the corner. Anterior crossvein at or near the middle of the discal cell. The axillary lobe is narrow, the alula large, the anterior half of the wing bears numerous, short, dark scales, except on the outer third. Costal comb moderately well developed. Ambient vein complete.

Abdomen: The abdomen is elongate, subcylindrical with parallel sides; at the base nearly but not quite as wide as the thorax. In length it is not quite as long as the wing. The ground color is shining blackish and is rather densely covered usually by black, short, suberect, more or less appressed, broad scales widely down the middles of the tergites and with large patches of white, gray, or yellow scales sublaterally, which vary from fine and narrow and mixed with fine, erect hairs, to wider scales on the fifth and remaining tergites. Last few tergites likely to have tufts of dense, long, wide, erect black scales. The terminalia are not turned downward but are recessed into the apex of the abdomen. I find 7 tergites in the male. There is no band of short hair beneath the scutellum but there is dense, erect hair laterally outside the scutellum.

The male terminalia from dorsal and lateral aspect, epandrium removed, show a large basally widened aedeagus. The dististyli are short and stout, turned backward medially with an apical notch, and the basistyle apparently has an underlying spoonlike apical process. Epandrium is quite short, high, subtriangular.

Material studied: A considerable series of the type-species and some material of three other species are before me, also pupae obtained by breeding.

Immature stages: These flies live in the nests of wasps. See discussion under life histories.

Ecology and behavior of adults: These flies have a somewhat bouncing flight. I have only seen one attempt at mating. Commonly found in Lafayette County, Mississippi, on flowers of *Rhus* spp., *Rudbeckia hirta* Linné, on sneeze weed, *Helenium tenuifolium* Linné, on *Apocynum cannabinum* Linné, and on devil's-walking stick, *Aralia spinosa* Linné. Found once 'as late as October on *Aster* sp. Robertson (1928) recorded these flies appearing upon *Bidens aristosa* (Michx.) Britt., *Rudbeckia submentosa* Pursh., *Rudbeckia triloba* Linné, and *Coreopsis tripteris* Linné.

Distribution: Nearctic: *Lepidophora lepidocera* (Wiedemann), 1828 (as *Toxophora* [= *aegeriiformis* (Westwood), 1835 (as *Ploas*), = *appendiculata* (Macquart), 1846 (as *Toxophora*)] ; *lutea* Painter, 1962.

Neotropical: *Lepidophora acroleuca* Painter, 1930; *culiciformis* Walker, 1850; *cuneata* Painter, 1939; *secutor* Walker, 1857; *retusta* Walker, 1857.

Genus *Cyrtomyia* Bigot

FIGURES 88, 319, 541, 584, 736, 745, 749, 872, 873, 874

Cyrtophorus Bigot, Ann. Soc. Ent. France, ser. 3, vol. 5, p. 292, 1857. Type of genus: *Cyrtophorus pictipennis* Bigot, 1857, by monotypy. Preoccupied by Le Conte in Coleoptera, 1850. *Cyrtomyia* Bigot, Ann. Soc. Ent. France, ser. 7, vol. 2, p. 340, 1892. Change of name.

Large, black flies with beautifully mottled wings, arched thorax, and somewhat decumbent abdomen. They are related to *Lepidophora* Westwood, through the fact that they both have scales upon the wing, a globose head, and a characteristic type of elongate antenna. *Cyrtomyia* Bigot differs by not having scales upon the antenna, and by a more generalized wing. The discal cell in *Lepidophora* Westwood shows a strong, rectangular bend in the fourth vein below, and the second vein and anterior branch of third vein each are very strongly bent near their ends at the apex of the wing. The flies of the genus *Lepidophora* Westwood are much more strongly arched and humped and the abdomen more strongly decumbent. The abdomen of *Cyrtomyia* Bigot is shorter, broader at the base. Both have strong, conspicuous bristles on thorax, scutellum, and upon all tibiae. The posterior femur bears strong, stout bristles; its tibiae with stout, spiculate bristles. Both *Cyrtomyia* Bigot and *Lepidophora* Westwood superficially resemble *Toxophora* Meigen in the decumbent aspect of head and abdomen, but differ conspicuously in the lack of long, curved, stout macrochaetae on the prominent prothorax of *Toxophora* Meigen, in the different venation, in the stout femora which are not swollen as in *Toxophora* Meigen. They also differ in the presence of bristly hairs along the sides of the oragenal cup.

The two known species of *Cyrtomyia* Bigot are from the southwestern part of the Neotropical region.

Length: 13 to 15 mm.

Head, lateral aspect: The head is subglobular, the face but little produced although the oragenal cavity extends well out from the eye margin, it also extends almost but not quite to the antenna, so that the face is quite short in the middle. Front and face continuous and both with rather dense, erect, long, distinctly bristly though slender, blackish pile extending out to the eye margins and continued down upon the whole of the gena leaving a small area beneath the eye which is bare and pollinose only. This bristly pile is not quite as dense upon the front and it is a little shorter on the upper front but a few of these elements are even stouter.

The occiput is quite swollen and prominent but without central cavity. The posterior eye margins are entire, the eye itself convex and inwardly retreating along its posterior border. The occiput is conspicuously covered with dense, long, and fine pile below in the middle which is shorter opposite the ventral eye corners. However, widely over the middle of the lateral occiput, there are long, conspicuous, quite scalfiform hairs that arise medially and become shorter, appressed scales near the eye margin. Also there is a tuft of reddish, medial hairs. Dorsally there is a dense clump or cluster of erect, black, spikelike bristles on each side of the dorso-lateral occiput. They rise above the ocellar tubercle. Palpus long and conspicuous with at least 2 segments; the outer segment is long and tapered apically. It extends as far as the beginning of the labellum on the proboscis. Dorsally and laterally the palpus bears numerous, moderately long, oblique setae, which are still longer at the apex. The proboscis is large, laterally compressed, with quite large, flattened labellum bearing a dorsal and ventral row of erect, fine setae. The proboscis is about $1\frac{1}{2}$ times as long as the head or twice as long as the eye. The eye itself is almost exactly hemicircular and quite plane posteriorly. Antenna attached near the upper fourth of the head, unusually long and conspicuous. The first two segments have conspicuous, dense, long, bristly pile on all sides. The first segment is 3 or 4 times as long as the second; the second segment is narrowed basally, somewhat dilated quite near the apex and about twice as long as its apical width. Third segment slender, gently narrowed from the base and about $2\frac{1}{2}$ times as long as the second segment; there is no microsegment and no pile is present.

Head, anterior aspect: Genofacial space about one-third the head width with parallel sides or even slightly widened between the lower eye corners. Front flattened, without medial groove, and very slightly raised above the eye margin. On each side in the middle it bears a longitudinal row of 4 or 5 stout, long bristles. The ocellar tubercle is quite low and rather small, but with a few, slender, bristly hairs between the ocelli. The oral opening is wide and very short oval. The head is only about as wide as the posterior thorax.

Thorax: The thorax is distinctly longer than wide, gently arched, and equally arched in front and behind. Mesonotum with rather dense, pale, flat-appressed, scales and scaliform pile, together with considerable, erect, moderately long pile. The pile in the middle is remarkably fine, the pile anteriorly and on the sides becomes coarser and intermixed laterally with long, conspicuous bristles. Some of the bristles on the lower humerus are quite stout but on the notopleuron there are 4 or 5 bristles and on the postalar callosity 3 remarkable, quite long, basally stout, curved, attenuate, reddish bristles. Margin of scutellum with a conspicuous row of long, basally stout, curved, black bristles and the disc is plastered with appressed, white scales. Pleuron shining and mostly bare. Upper mesopleuron and its posterior corner with dense tufts of fine, long, crinkled, white pile, and below it some similar reddish hairs. Metapleuron bare. Hypopleuron with a tuft of quite long, fine, reddish hairs. Squama large with a long fringe of fine hairs. Halteres with cup-shaped excavation apically, the stalk bearing scaliform pile.

Legs: The femora are relatively short but stout with fine setae and more numerous, appressed scales. Especially on the hind femur, ventrally, there are many long, fine hairs. Anterior femur with 2 stout bristles ventrally at the apex, posterior femur with an antero-ventral row of some 12 stout, long, oblique, black bristles. All tibiae with long, stout spicules placed in 4 rows; each row contains about 7 elements. Claws slender, pulvilli long, arolium minute.

Wings: The wings are rather broad, narrowed at the base and strongly mottled with sepia brown. There are 2 submarginal cells; the marginal cell is bulbous at the apex. The 4 posterior cells are widely open, the anterior crossvein enters the discal cell at or near the outer third, and the medial crossvein makes a strong but rounded bend basally, otherwise narrowing the long, distal cell much as in *Lepidophora* Westwood. Anal cell closed at the margin, axillary lobe quite long, the alula large, hemispherical with a short fringe. At the apex of the radial sector is a patch of broad, reddish-brown scales and others along the costal cell, and proximal to the arculus.

Abdomen: The abdomen is broad at the base and rather flattened, and as wide or wider than the thorax and gently narrowed toward the blunt, upturned apex of the abdomen which leaves a transverse depression across the middle. Tergites with dense, suberect, bristly pile, and likewise with rather dense scales; these scales are white in a band across the middle, brown or blackish elsewhere.

The male terminalia from dorsal aspect, epandrium removed, show a wide and short-oval structure, with a long, basally expanded, apically clublike, apically incised dististyle which suggests a crab's claw in appearance. The epiphallus is wide and conical, the basal part of the aedeagus also very wide. From the lateral aspect, the basistylus is long and stout, the epiphallus particularly wide, equally wide apically but rounded.

From the lateral aspect, the dististyli are quite short. The epandrium is short, but high, and is triangular.

Material studied: Consists of both the known species; found in the British Museum (Natural History), and material received from a collector.

Immature stages: Unknown. Probably similar to *Lepidophora* Westwood.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical: *Cyrtomyia chilensis* Parnamonov, 1931; *pictipennis* Bigot, 1857.

Genus *Marmasoma* White

FIGURES 89, 313, 542, 578, 878, 879, 880

Marmasoma White, Papers Proc. Roy. Soc. Tasmania, p. 188, 1917. Type of genus: *Marmasoma sumptuosum* White, 1917, by monotypy.

Medium-sized flies with moderately humped thorax. The head is rather more decumbent than the abdomen but both are drooping; the latter is relatively about as elongate as in *Lepidophora* Westwood but a little more slender. Unlike the other genera of the family the antennae are relatively shorter in all segments, especially the second, and the antennae have only slightly widened hairs, not conspicuous scales and scaliform pile. Also, it should be noted that this genus has the anal cell widely open and there are spiny bristles on the femora in both sexes. The female front has a whole row of conspicuous bristles on each side, not just a curved pair as in *Toxophora* Meigen. The wings are spotted. The prothorax is much less prominent than in the other genera. I do not feel that the genus is particularly close to the other genera of the subfamily; certainly the general form and the size and shape of the wings more suggestively resemble *Lepidophora* Westwood.

These flies are known only from Tasmania and Western Australia.

Length: 10 to 12 mm.; of wing 7 to 8 mm.

Head, lateral aspect: The head is subglobular, the occiput very strongly developed posteriorly, especially on the upper part. The occiput bears long, coarse, non-bristly pile, but intermixed with it broadly over the whole upper surface are numerous, black, long, blunt, spikelike bristles and near the eye margin is a fringe of short, appressed, scaliform hairs touching the eye. The front and vertex are plane with the eye, but the small ocellar tubercle is quite raised; the latter bears 2 or 3 strong, long, black bristles curved forward and on each side of the upper half of front and vertex is a regularly spaced row of some 6 or 7 very long, curved, sharply attenuate, stout, black bristles directed forward. The eye is very large, the posterior margin plane, with a slight overgrowth posterolaterally as in *Toxophora* Meigen.

The face is short, but extends downward rather more than twice the length of the second antennal segment. The linear genal area is obscured by an overgrowth of

the eye. The proboscis is long and slender, longer than the head, the labellum is likewise slender with a few fine, erect, widely spaced, bristly hairs laterally. Palpus long and slender, the second segment clavate and at least half as long as the first segment. The whole palpus is nearly half as long as the proboscis. The antennae are attached at the middle of the head and are elongate but not as long as in *Toxophora* Meigen. The cylindrical first segment is pollinose, 5 or 6 times as long as wide, and bears long, shaggy, pale pile laterally and below with shorter pile dorsally, and with a few fine, black, bristly hairs dorsally. Second segment short and bead-like, cylindrical, third segment knobbed at the base and at this point much more narrow than the second segment. Third segment knobbed at the base, gradually widened until at the basal fifth it is as wide or slightly wider than the second segment and from this point it is gradually narrowed, the apex is not quite as wide as the base. The apex bears 2 microsegments, the second microsegment bears an apical spine and is slightly longer and more attenuate than the basal microsegment. Third segment of male antenna without the medial, elongate patch of silvery reflecting pollen.

Head, anterior aspect: The head is short oval in females, nearly circular in males, scarcely wider below than above. The eyes are widely holoptic in the male, the front is reduced to a small triangle, the eyes meeting a distance of about 3 times as long as the frontal triangle. Eyes in the female widely separated, the sides of the front are not quite parallel, widening slightly toward the antennae and the vertex a little more than twice as wide as the ocellar triangle. The antennae are very narrowly separated at the base but converge and touch. Face from the frontal aspect nearly as extensive as in *Toxophora* Meigen, pollinose only, and with a deep crease proceeding from near the middle of each antennae obliquely downward toward the eye margin so that the lower part of the face laterally presents a vertical wall, and the crease on the lower part disappears into a narrow, tentorial fissure. Gena occluded, except at the very bottom of the eye where it is linear. Oragenal cup exceptionally deep, especially below, but slanting upward toward the face as in *Toxophora* Meigen, but however without the double wall and enclosed lateral space.

Thorax: The thorax is 3 or 4 times as long as the head, strongly humped and convex both in front and behind. It is even more convex than *Lepidophora* Westwood and the large, rather flattened scutellum is more strongly sloped downward and backward. The head and abdomen are even more decumbent.

The mesonotum is black with the lateral margins brown, quite opaque, the surface densely covered with microscopic scales, the pile consisting of matted, rather long, tangled, slightly flattened hairs, dense anteriorly, more loose behind the humerus and forming a short, transverse, more erect band of pile across the front of the mesonotum and leaving the middle of the mesonotum narrowly black with a few black hairs. The mesonotum

bears an extensive patch of scattered, curved, basally stout, apically sharp macrochaetae that cover almost the whole of each lateral half of mesonotum lying in front of the deep, sharply creased, transverse suture. The macrochaetae are smaller than in *Toxophora* Meigen. On the notopleuron is a longitudinal row of 4 much stouter and longer macrochaetae and a similar row of 4 above the wing, 2 on the postalar callosity, a patch of 4 on each side in front of the scutellum, which represent continuation of middorsal rows. The margin of the scutellum has 5 or 6 pairs that are more slender. Discal pile of the large, hemicircular scutellum similar to that of the mesonotum. The postalar callosity is large, pollinose, and with a tuft of pile above and a tuft of pile below.

As in *Lepidophora* Westwood the humerus is unusually elongate, extending far backward from the anterior margin of the mesonotum. The pronotum, however, unlike other members of the subfamily Toxophorinae is very small, not prominent; nevertheless the neck or cervical region seems to be fairly long and the propleuron rather extensive with a pair of very long, strong macrochaetae. Squama quite short, except on the alary portion. The entire border is thick and ridgelike, the alary portion membranous, triangular, with a fine, short fringe of hairs. The thoracic portion is quite long and with a medial strigula. Halteres comparatively small, the knob larger with basal crease above and with cup-like depression apically. The pleuron is largely bare, except for the pollen; the upper half of the mesopleuron has rather dense pile, the lower part a few scattered hairs, and there are a very few hairs on the upper sternopleuron. The lateral metanotum has much long pile and also has 4 or 5 macrochaetae. The metapleuron is bulbously swollen with vertical fringe of pile and 7 or 8 long, slender, black bristles. Likewise, a dense tuft of pile is behind the spiracle, but the hypopleuron and the pteropleuron are bare.

Legs: The legs are comparatively short, the anterior and middle femora distinctly though gradually thickened from apex to base; hind pair stout but not swollen. The anterior femur has 1 bristle posteriorly near the apex and a few fine, long, erect hairs below. It is rather densely covered with large, broad scales above and also below, fewer laterally and behind. Middle femur similar in its fringe of hairs and scales but with 2 stout, subapical spines, one in front and one behind. Hind femur with many scales, almost no fine hairs, but with a ventrolateral row of 8 or 9 oblique and curved, stout, black, spinous bristles. Also there are 12 or more shorter, finer bristles ventrally, 3 dorsolaterally on the outer half, 2 small and 1 very large bristle dorsomedially near the apex. The anterior tibia has many scales and fine, oblique, ventral setae below on the outer half and with 3 rows of prominent, stout, spiculate bristles, somewhat irregularly placed; the anterodorsal row has 8 or 9, the posterodorsal row has 6 or 7 and the posteroventral row has 10; the apical spines are prominent. The middle tibia is similar but the bristles are much stouter and

longer. There are at least 6 very large ones antero-dorsally and on the basal half there are 3 very large, posteroventral bristles. Hind tibia similar to the middle tibia. There are 5 exaggerated bristles anterodorsally ending at the outer third. The tarsi have small scales; basitarsi with a few, very large, spinous bristles on the middle pair. Remaining segments with comblike, stout setae ventrally. Claws long, rather sharp, curved on the outer half, the pulvilli large and long.

Abdomen: The abdomen is elongate but only about $1\frac{1}{2}$ times as long as the thorax; it is much narrower than the thorax beyond the first segment but with nearly parallel sides beyond the third segment so that on the whole the abdomen appears subcylindrical. The tergites are covered with moderately long, flat-appressed, pale scales, which are apt to be largely denuded over most of the tergite, but are apt to persist as a narrow fringe along the posterior margins, and especially below on the lateral margins. On the second to fifth tergites on each side is a row of black, shining, punctiform dots, sometimes a double row. There are some scanty long, fine, erect hairs ventrally on the anterior half of the abdomen. The sternites are apt to be compressed; the whole abdomen is slightly compressed. Male terminalia small, scarcely protruded and not prominent. Last sternite troughlike with triangular apex. There are 8 well-developed tergites present in the males the last ones shorter, but beyond this the ninth tergite comprising the hypopygium is large and elongate, steep laterally with the small genitalic valves appressed.

The male terminalia from dorsal aspect, epandrium removed, show the structure extraordinarily long and

slender. The basistyli apically extend beyond the attachment of the long, medially bristly, apically obtuse dististyli, which, however, at the apex have a small process, convergent and turned inward. Epiphallus forming a split sheath, the ejaculatory process spade-shaped. From the lateral aspect, the basistylus is quite bowl-shaped, the dististylus rather small, the apical prong also visible, but the epiphallus forms a very long conspicuous, snakelike, S-shaped process, especially curved downward and then backward at the apex. The epandrium is curious in having a conspicuous, ventral, basal process directed backward rather than downward.

Material studied: The type-species.

Immature stages: Unknown.

Ecology and behavior of adults: Not recorded.

Distribution: Australian: *Marmasoma sumptuosum* White, 1917.

Genus *Palintonus* François

Palintonus François, F. J., Bull. Ann. Soc. Roy. Ent. Belgique, vol. 100, p. 324, 1964. Type of genus. *Lepidophora austeni* Paramonov, 1949.

Very recently François transferred the Central African fly *Lepidophora austeni* Paramonov to a new genus, which he calls *Palintonus*. I have not seen this genus.

Material available for study: None.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Palintonus austeni* (Paramonov), 1949 (as *Lepidophora*).

Subfamily Systropinae Brauer, 1880

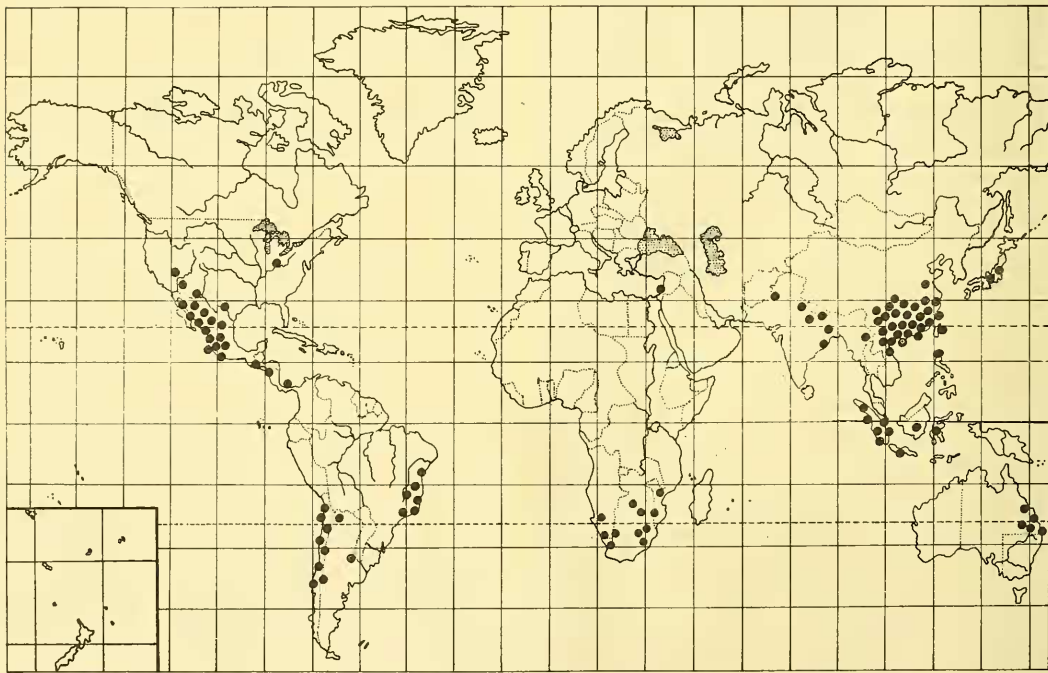
The flies of this subfamily are unique and very beautiful. They are remarkable examples of mimicry of sphecoid and vespoid wasps and the group extends into all the world regions. Most of these flies are parasitic in the larval stages upon moths of the family Enclidae, but one species from Central Africa has been reared from cocoons of *Stenomutilla beroe* Pering.

The flies of this subfamily are unique in several respects. They are distinguished by: (1) the long or very long, thin, abdomen, either cylindroid or laterally compressed in females, clavate in males, together with the extraordinarily extensive and lengthened and thickened metasternum in *Systropus* Wiedemann, but ordinary in *Dolichomyia* Wiedemann; (2) the unusually prominent eyes which are often holoptic in both sexes with consequently reduced facial and clypeogenal area;

(3) the long, slender, distally flattened, approximate antenna, shorter in some genera, together with the slight but distinctly concave occiput; and (4) the slender wing with only 3 posterior cells and reduced axillary lobe and alula. There are either 2 or 3 submarginal cells.

Other characters of the subfamily that may be noted are the slender wings with axillary lobe either narrowed or completely wanting so that the wing appears to be almost stalked. There is no special pronotal development as in the Toxophorinae but the propleural lobes may be quite swollen. The proboscis varies from as long as the head to much longer. These flies appear to be quite bare but are clothed with fine, minute scales, which may be in regular transverse rows upon the legs, or scattered hairs and pollen. The first posterior cell is

SYSTROPINAE



TEXT-FIGURE 34.—Pattern of the approximate world distribution of the species of the subfamily Systropinae.

narrow and is open or narrowly closed, and the anal cell when present is closed and sometimes petiolate. There is a nodelike thickening at the origin of the marginal cell and in some the radial sector has become so shortened that it is very short and vertical. A strigula is characteristically present and prominent, often colored pale. General coloration ranges from smoky blackish species to others black with conspicuous pale yellow or white humeral and propleural spots, others with base of abdomen reddish as in ammophiloid wasps, still others that are a beautiful orange red or brown with paler spots. One South American species has the metasternum pale yellow with 4 black spots. Characteristically there are dorsolateral metasternal spines.

Brues (1939) notes that the East Indian species are more apt to mimic vespoid wasps; whereas, occidental species are more apt to resemble the wasps of the genus *Spheg* (*Ammophila* of authors).

The genus *Systropus* Wiedemann has been subdivided by Enderlein (1926) into a number of minor groups; while it might have been better to leave these subdivisions as "species groups" he has proposed names for 7 subgroups on the relative separation of the eyes in males and females, the number of submarginal cells and the number of segments in the abdominal petiole. While the number of submarginal cells has been appropriately used in many groups of bee flies, and even though it is to a minor extent admittedly unstable in some groups, in many genera it is a very useful character. It does indicate stepwise the strong tendency of the dipterous wing toward simplification and vein reduction.

KEY TO THE GENERA AND SUBGENERA OF SYSTROPINAE

1. Metasternum entirely normal. Abdomen laterally compressed throughout its length, the tergites with opaque black spots, saddlelike above. Abdomen not narrowed at base more than at apex. Axillary cell absent. Subcostal cell occluded until the adjacent veins lie almost side by side 2
 - Metasternum grossly and remarkably swollen, enlarged, projecting and drawn out posteriorly. The abdomen is long, very slender, and attenuate toward the base, more or less widened posteriorly. Wasplike flies of remarkable appearance. Axillary cell present but alula absent. First antennal segment extraordinarily long, almost threadlike; other segments are also lengthened . . . *Systropus* Wiedemann
 2. First antennal segment twice as long as second. Hind femur remarkably swollen distally. No anal vein present. Metasternal plate shelflike, with spine or 1 or 2 teeth.
Zaclava, new genus
- First antennal segment 4 or more times as long as the second.
Hind femur not or scarcely thickened distally. A well-

I leave to the bee fly students of the future the matter of usage of these names proposed by Enderlein as genera and which I leave as subgenera since they are already in the literature; I have indicated their definition as subgenera as included in my key to the subfamily.

There is one well-differentiated additional genus in this subfamily. I refer to *Dolichomyia* Wiedemann with type-species from Colombia. It occurs also in the western United States, in Chile, and Australia, but the species in Australia, of which I have collected 2, are not conspecific and for them I have erected the genus *Zaclava*. All of these flies are much smaller than most species of *Systropus* Wiedemann.

This subfamily is chiefly tropical in distribution. Only 5 species are found north of Mexico and none in Europe proper.

The Systropinae are characterized by a broad hypopygium which is elongate oval without being exceptionally elongate. From the dorsal aspect there is a strong, wide bridge across the middle overlying the epiphallus, from which arises two pairs of peculiar lobe-like, apically pointed structures that we here term superior and inferior claspers. The dististyli are quite large, widened apically and blunt. Epandrium very large and subrectangular. In the tribe Dolichomyini, which should possibly be elevated to a subfamily, and this I would be reluctant to do for reasons stated in the section on the general phylogeny, there are none of these accessory processes and lobes and claspers. Also the dististyli are rather curious.

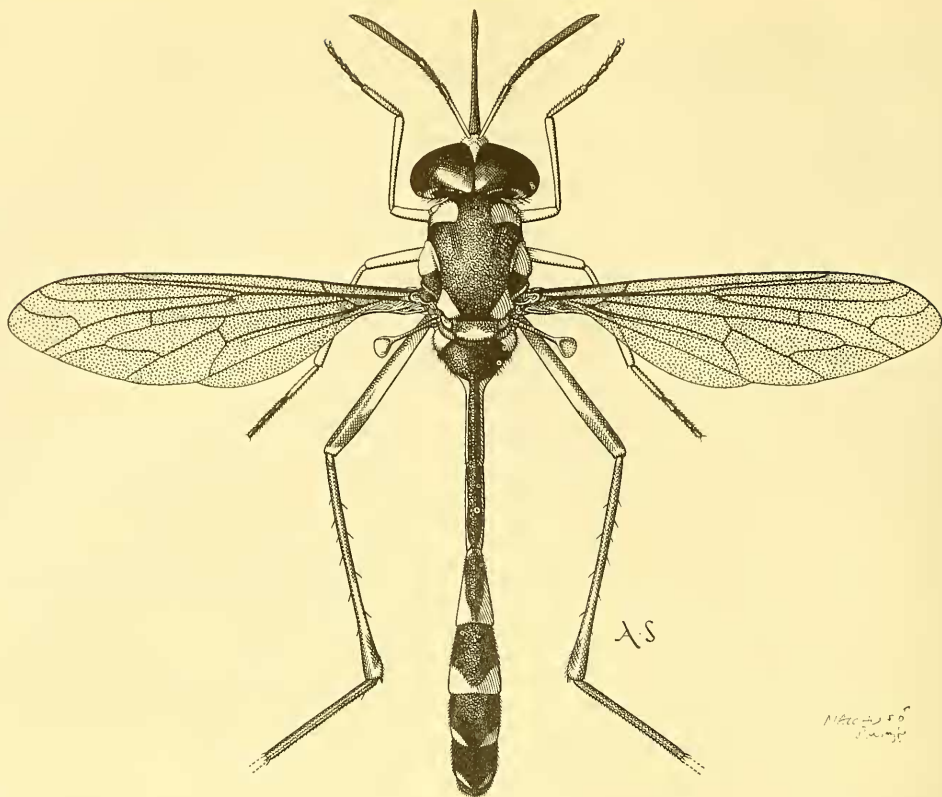
- developed anal vein present. Metasternal plate scarcely noticeable *Dolichomyia* Williston
3. Two submarginal cells. *Systropus* Wiedemann, sensu stricto
(If eyes of male and female completely holoptic, the subgenus *Cephenus* Enderlein.)
 - Three submarginal cells; eyes of female in contact above. *Systropus* (*Coptopelma*) Enderlein
 - Three submarginal cells; eyes of female separated above. *Systropus* (*Diaerops*) Enderlein
 - Three submarginal cells; abdominal petiole 2-segmented. *Systropus* (*Dimelopelma*) Enderlein
 - Three submarginal cells, abdominal petiole with 3 or 4 segments; eyes of female separated above. *Systropus* (*Coptodierus*) Enderlein
 - Three submarginal cells; abdominal petiole with 3 or 4 segments; eyes of female in contact above. *Systropus* (*Symballa*) Enderlein

Genus *Systropus* Wiedemann

FIGURES 86, 87, 336, 565, 588, 887, 888, 889

- Systropus* Wiedemann, Nova Diptorum Genera, p. 18, 1820.
Type of genus: *Systropus macilentus* Wiedemann, 1820, by monotypy.
Systrophus Latreille, Familles naturelles du règne animal, p. 496, 1825.

- Céphène* (Vernacular) Latreille, Familles naturelles du règne animal, p. 496, 1825. "Change of the name *Systrophus*, of Latreille, under the presumption that it was preoccupied by *Systropha*, Illiger 1806, Hymenopt."—Footnote, Bezzi, p. 3, 1924.
Cephenus Berthold, Natürliche Familien des Thierreichs (German translation of Latreille, 1825), p. 506, 1827.
Systrophopus Karsch, Zeitschr. Berliner Ent. Ges. Naturwissensch., vol. 53, p. 656, 1880.



TEXT-FIGURE 35.—Habitus, *Systropus (Cephenius) maccus* Enderlein, from a male paratype.

Cephenus Karsch, Zeitschr. Berliner Ent. Ges. Naturwissensch., vol. 53, p. 656, 1880.

Systropus Verrall in Scudder, Nomenclator Zoologicus, p. 355, 1882.

Cephenius Enderlein, Wiener Ent. Zeitung, vol. 43, p. 70, 1926b. Type of subgenus: *Systropus studyi* Enderlein, 1926a, by original designation.

Coptodierus Enderlein, Wiener Ent. Zeitung, vol. 43, p. 91, 1926b. Type of subgenus: *Coptodierus vespiformis* Enderlein, 1926, by original designation.

Coptopelma Enderlein, Wiener Ent. Zeitung, vol. 43, no. 2, p. 70, 1926b. Type of subgenus: *Systropus (Coptopelma) schineri* Enderlein, new name for *Systropus macilentus* Wiedemann, as misidentified by Schiner. See Hesse, pp. 1001-1002, 1938.

Diaerops Enderlein, Wiener Ent. Zeitung, vol. 43, no. 2, p. 70, 1926b. Type of subgenus: *Systropus marshalli* Bezzi, 1924, by original designation.

Dimelopelma Enderlein, Wiener Ent. Zeitung, vol. 43, p. 90, 1926b. Type of subgenus: *Dimelopelma tessmanni* Enderlein, 1926, by original designation.

Pioperina Enderlein, Wiener Ent. Zeitung, vol. 43, no. 2, p. 70, 1926b. Type of subgenus: *Cephenus femoratus* Karsch, 1880, by original designation.

Symballa Enderlein, Wiener Ent. Zeitung, vol. 43, p. 92, 1926b. Type of subgenus: *Systropus leptogaster* Loew, 1860, by original designation.

Osten Sacken (1887), p. 157, key to 11 species from Mexico.

Williston (1901), pp. 292-297, key to 5 species from Mexico.

Bezzi (1924), p. 117-118, key to 9 Ethiopian species.

Enderlein (1926), pp. 71-75, key to 34 Palaearctic and Oriental species (as *Cephenius*).

Curran (1930), p. 51, key to 18 Neotropical species.

Engel (1933), pp. 87-89, key to 20 Palaearctic and Oriental species (as *Cephenius*).

Hesse (1938), pp. 996-1001, key to 10 male and 7 female South African species.

Painter and Painter (1963), pp. 287-290, key to 24 species and 5 subspecies, Nearctic and Neotropical.

Strange and beautiful flies, which have developed an astonishing pattern of mimicry centered around several groups of elongate, hunting wasps. The American species have centered around caterpillar-philic wasps of the sphecid genus formerly called *Ammophila* Kirby, now known as *Sphex* Linnaeus. Certain oriental and Indomalaysian species have been likened in appearance to vespids. Hesse (1938) likens the shape to wasps of the genus *Sphex* Linnaeus, *Sceliphron* Klug, or *Belonogaster* de Saussure.

Flies of the genus *Systropus* Wiedemann are noteworthy for both their extraordinarily slender, laterally compressed, lengthened, petiolate, apically enlarged abdomen, very long hind legs, and very long, slender antennae; together with an extraordinarily bare, denuded appearance due merely to the reduction of pile to the status of minute, flat-appressed, stubby setae. Also, the metasternum is greatly enlarged, heavily sclerotized, and slanted obliquely upward. The coloration of the American forms is more commonly black with yellow spots on propleuron, humerus, notopleuron, postalar callosity, or sometimes a combination of these areas. Nevertheless, a few American species tend to be in considerable part light reddish, or yellowish on the abdomen. One Madagascar species is entirely a beautiful, brownish, orange yellow with 4 conspicuous black spots across the anterior thorax.

The venation in the genus is simple, but noteworthy for its slender wing, narrowed at the base, in which there are only 3 posterior cells; wing hyaline, sometimes smoky. The proboscis is long and quite slender with long, slender labellum, used to probe florets.

The genus is almost worldwide in distribution, more abundant in hot, wet parts of the world. It is peculiar that no species are known from Europe, even in its southern extremes, nor yet North Africa, because the American *Systropus macei* Loew extends northward in the east to Connecticut, at a latitude of about 42 degrees and westward as far as Minnesota. There are 3 species known from North China, and 6 from Sikkim, which at latitude near 30 degrees north is equivalent to Arizona and northern Mexico from where several species are known; the genus appears to be a little more plentiful in tropical and subtropical regions both above and below the equator.

Length: Including antennae 12 to 26 mm. with most species about 15 to 20 mm.

Head, lateral aspect: The head is unique in that it is composed almost entirely of the eye with relatively small frontal and facial areas, and with no occiput visible in lateral profile. The posterior eye margin is nearly plane, perhaps very slightly concave from the top down to the lower third, for the attachment to the cervix of the thorax is distinctly below the middle of the head. Viewed posteriorly the occiput is very slightly and shallowly concave and there is a narrow, vertical groove on the upper part, well below the vertex, and continued by a medial line up to the vertex. The ventrolateral tentorial fissures are mere shallow creases. The head is relatively short, the anterior eye margin is hemicircular in form but the whole head is much less than half a circle. Hence, the head and eye are relatively short. The occiput is pollinose only on the upper three-fourths of the head or more, but sometimes there are a few, fine, suberect hairs ventrally on the lower occiput. The front is small and plane with the eye, and at the base of the antennae extends forward only a very short distance; consequently the upper face is also very limited in extent. The oragenal cup is low and short, but extends

nearly to the base of the antennae, leaving a small, medial, facial area.

The proboscis is long and exceptionally slender, always longer than the head, but seldom extending beyond the antennae. It varies from about twice the length of the head to about 3 or 4 times the head length. The labellum is equally slender, a third the length of the proboscis or even more with the lobes divergent, often with curled apices. Palpus visible, minute, elongate, pointed, slender, cylindrical or more or less flattened, with scarcely observable hairs and rather deeply recessed within the oragenal cavity, and composed of a single segment. The antennae are attached at or just above the middle of the head and are remarkably elongate, and quite slender, especially the first two segments. The first segment is longer than the head, sometimes nearly twice as long; the second segment varies from a third to a fifth of the length of the first segment; both segments have short, dense, appressed setae but they are a little longer and more evident on the second segment. The third segment is always strongly flattened, either elongate lanceolate, or elongate oval. The relative proportions of segments may be variable in some species.

Head, anterior aspect: The head is circular, or slightly narrowed from above and much wider than the thorax. The eyes of the male are holoptic for a very considerable distance, leaving a small, low, pollinose, or micropubescent frontal triangle and a still more minute vertical triangle which is composed entirely of the ocellar tubercle. The small ocelli lie on the eye margin and form nearly an equilateral triangle. The ocellar tubercle is a little swollen and raised. The lateral ocelli may be smaller. Oddly, the eyes are often holoptic in the female, though to a more limited extent, leaving the front extending farther upward and forming a very long, slender, wedge-like triangle. In some species the front and face can scarcely be seen from the lateral aspect. Below the antennae the face is about as long as wide, pollinose, with a very few, fine, erect hairs. The oragenal cup is long, quite deep, wedge-shaped, with steep vertical sides on the interior. The outer wall is short, slightly sloping and poorly separated from the long, quite deep sloping upper face and the narrow, ventral gena; middle of gena below with tentorial fissure barely indicated. The antennae are attached adjacent.

Thorax: The thorax is relatively short and compact, the mesonotum very little longer than wide and slightly convex. The wings are attached far to the rear of the thorax, and in fact almost above the haltere. The propleuron and mesopleuron are compacted and compressed below and crowded to the front of the thorax. The metasternum and metapleuron are extremely large, elongate, and obliquely extended upward and heavily sclerotized. The pile of the mesonotum is quite minute, rather abundant, stubby or setate, some of it erect, some of it curled backward. Some species have slightly longer, fine, erect pile over the mesonotum. There is a

flangelike lateral plate from the notopleuron resting over the base of the wing. This notopleural flange has a wide, sunken fascia which in some species is densely covered with rather long, erect, bristly pile. The humerus forms a large, triangular, vertical plate, very short in length seen from above, and covered with pile corresponding to that of the pleuron. The scutellum is comparatively small, with curled setae and a little longer marginal pile; it is sometimes bimammillate, or in some species it and the mesonotum as well are coarsely punctate. The metanotum is pollinose only, and there is often a curious, coiled, or basal, scalelike or flatlike extension to the squamae on either side at the base of the scutellum. This curious structure as Painter and Painter (1963) note was called the strigula by Williston (1901), the membranous tubercle by Verrall (1909), the scutellar callosity by Bezzi (1924), and the foliate scutellar callosity by Hesse (1938).

Mesopleuron with erect or appressed pile of no great length. Pteropleuron and metapleuron both pilose. Sternopleuron micropubescent or pollinose only. Propleuron swollen and domelike to a varying extent in species both from the Old and New Worlds. Squamae very short with a short fringe.

Legs: The anterior four legs are nearly equal in size. Both their femora and tibiae are nonspiculate and have dense, appressed micropubescent. Hind legs greatly elongate and much lengthened; they are at least twice as long as the middle pair of legs, sometimes more. The hind femur varies from slightly swollen distally to other species in which it is twice as wide subapically as basally. The pile consists of very minute, appressed setae curiously laid down in transverse rows so that there is a shinglelike effect. In addition there are appressed or erect setae of greater length and stoutness. The hind tibia bears dorsal, lateral, and ventral rows of stout, sharp, spinous bristles of no great length, the number of bristles ranging from 4 to 7; pulvilli large, broad, nearly as long as the claw. The claws are sharp and strongly curved at the apex.

Wings: The wings are elongate, somewhat narrowed at the base, the axillary lobe quite long and evenly curved at base and apex. There are 2 or 3 submarginal cells, usually only 2, and only 3 posterior cells, all open. The anterior crossvein enters the discal cell beyond the middle, the anal vein is closed and stalked and the alula is absent or reduced to a mere linear strip. The base of costa has a round scale. The whole wing is villose, sometimes tinted with smoky brown diffusely about the middle at crossveins or furcations.

Abdomen: The abdomen is elongate and slender, cylindrical or laterally compressed beyond the first segment. The first segment is short and triangular, never as wide as the mesonotum. At the base of the fourth segment the abdomen begins to widen dorsoventrally though often remaining conspicuously flattened and in other species more clavate. The size of the club formed by the seventh to eighth segment varies greatly. The pile is minute, flat-appressed, and rather dense. A little erect,

slightly longer pile is on the sides of the first segment. There are 8 visible segments in both sexes. Last female sternite quite variable; "either elongate and scoop-like, or with enclosed elongate process, or with 2 parallel lamellae, or shorter, emarginate apically, with the middle process projecting, or with merely a bifid process at the end of the abdomen" (Hesse, 1938). In the male terminalia the hypopygium is complex and peculiar. The last abdominal segment is so modified as to be closely associated with the true genitalic elements. This is true also of the genus *Toxophora* Meigen, and Hesse (1938) notes that it is also true of *Usia* Latreille. This last abdominal segment is produced on each side into a prong or process, and the genitalic structures are reversed leaving the last sternite dorsal in position, the last tergite ventral.

Hesse (1938) notes from his study of 11 South African species that the hypopygium of this genus is complex and the last abdominal segment modified to such an extent that it is more intimately connected than usual with the hypopygial structures proper, and that it plays a greater part in copulation than similar structures in other bombyliids. As in *Usia* Latreille and *Toxophora* Meigen the last abdominal segment is opposed to the hypopygium and is also produced into a prong or process, and the hypopygial structures are reversed in position so that the usual basal part is ventral, and the usual last sternite, which encloses the aedeagus in most other bombyliids, is dorsal in position and corresponds to the last tergite; apically its apical angle is produced into an elongated process, or prong, which is straight, curved or "hook-like." Hesse finds the apical margin of this tergite is usually emarginate and between the prongs, attached by a membrane, there is a triangular plate. Toward the inner side of each terminal plate he finds an oval, or elongate, sometimes very broad, callus-like structure, its surface roughened, filelike, or faceted; he views these and similar plates in other bombyliid genera as modified terminal abdominal segments. The hypopygium itself, he notes, "consists of a single basal part, more or less feebly divided into two parts by a medial depression, and apically each part ending in an apical segment (joint) which assumes many shapes in different species but usually ends in a spine-like beak directed inward."

The "aedeagus of the aedeagal complex, located in the hollow of the basal part is generally short, more or less concealed by the remainder of the armature, and consists of an aedeagal process which corresponds to the same of other bombyliids, an accessory process and a ramus." The aedeagal process, Hesse finds, is either quite prominent and inflated, or tumid, or more slender and bifid apically; the accessory process either leaf-shaped, twisted, or simply rodlike, or lobelike, and connected on each side to the basally directed aedeagal struts; the aedeagus passes on into the middle part which has the usual lateral strut on each side, and the medial, basally directed basal strut.

The aedeagus is also produced into a basally directed, flattened, strap-like, flattened, or boomerang-shaped aedeagal strut on each side in the hollow of the basal part and usually projecting basally a little beyond the base of the basal part. The whole aedeagal structure is joined on to the basal part on each side by means of the ramus, both together forming a jaw shaped or inverted U-shaped structure, the apical part of which may be broadened or produced into a lobe or spine on each side.

Hesse presents many excellent figures of the complicated genitalia of South African species. Painter and Painter (1964) give excellent illustrations of the male genitalia of five North American species and parts of others and figure females of some.

Dr. A. J. Hesse was able to study a very large assemblage of species in this genus; for this reason I quote his comments on the male genitalia:

Hypopygium of males is complicated and peculiar in that the last abdominal segment is structurally modified to such an extent that it is more intimately connected with the true hypopygial elements than in all the preceding genera. There appears no doubt that it thus plays a greater role in the copulatory act than homologous structures in other Bombyliids in this first division of this family. As in the case of the Palaearctic *Usia* and in the genus *Torophora* the last abdominal segment, opposed to the hypopygium, is also produced on each side into a prong or process. The hypopygial structures of *Systropus* are also constantly reversed in position in that the usual basal part of the hypopygium is ventral in position and the usual last sternite, enclosing the aedeagal structures in most other Bombyliids, is dorsal in position and corresponding to a last tergite. This latter segment, is usually somewhat sunk in or lower than the tergite before it and is alluded to as the last tergite. Apically on each side its apical angle is produced into an elongated process, prong, or spine which is straight, curved or even hook-like. The apical margin of the last tergite is usually emarginate and on each side between the prongs and attached by a membrane there is a subtriangular or triangular plate. Towards the inner side of each terminal plate above there is an oval or elongate and sometimes very broad, black, indurated, callus-like area, the surface of which is shagreened, file-like or appearing faceted. These and similar plates present in all other Bombyliid genera probably represent modified terminal abdominal segments.

The last tergite in *Systropus* is attached to the ventrally situated basal part of hypopygium on each side laterally and towards the base and also medially on the inside to the apical part of the hypopygial ramus of the aedeagal complex by a transverse, flattened, strap-like or band-like, chitinous band, extending from the base of one prong to the other and often produced towards the centre into an apically directed process or lobe on each side. The actual attachment to the apical part of the ramus is by means of a tough membrane.

The hypopygium itself consists of a single basal part more or less feebly divided into two parts by a slight medial depression. Apically each part ends in an apical joint which assumes a variety of shapes in the various species and usually ends in a sharp or spine-like beak directed inwards. The aedeagus of the aedeagal complex, lodged in the hollow of the basal part, is usually shortish and more or less hidden by the rest of the armature, consisting of an aedeagal process corresponding to the ventral aedeagal process of some other Bombyliids, an accessory process and the ramus. The aedeagal process is either very prominent, inflated or tumid apically, or more slender and bifid apically. The accessory process is either leaf-shaped and twisted or merely rod-like or lobe-like and is usually connected or joined on each side to the basally directed aedeagal struts. The aedeagus is also produced into a basally directed, flattened, strap-like or boomerang-shaped aedeagal strut on each side in the hollow of the basal part and usually projecting basally a

little beyond bases of basal part. The entire aedeagal structure is joined on to the basal part on each side by means of the ramus, both together forming a jaw-shaped or Ω -shaped structure, the apical part of which may be broadened or produced into a lobe or spine on each side.

The male terminalia from dorsal aspect, epandrium removed, show a broad, stout structure in which the epiphallus encloses the ejaculatory process which is much shorter and more slender and emerges below. A strong wide transverse bridge from the ramus emits 2 pairs of prominent lobelike claspers. The superior pair is curved inward at the apex, the inferior pair is curved outward. In the lateral aspect the dististyli are large, wide, blunt, and almost truncate at the apex, and wider apically. The claspers are very prominent and long and the epandrium quite large, subquadrate with a ventral, apical lobe.

Material available for study: The series of species of this genus in the British Museum (Natural History) and of the National Museum of Natural History, together with a representative of *arizonicus* Banks furnished me by Dr. George Byers, and of other material received by purchase from South Asia, South America, or Madagascar, besides several species from the United States and Mexico.

Immature stages: The flies of this genus are mostly parasitic on the larvae of the lepidopterous family Eucelidae (Limacodidae of authors), or in one known instance from the cocoons of the wasp *Stenomutilla beroe* Perring. See section under life histories for further discussion.

Ecology and behavior of adults: Adult flies of this genus are active flies, especially likely to be found around midday in hot sunshine coming to various flowers upon which they feed. Painter and Painter (1964) have found them occasionally as early as 10:30 A.M., as late as 4:00 P.M. Painter and Painter (1964) record Mexican species from the flowers of the following: *Baccharis glutinosa* Pers. (Compositae), the vine *Cissus rhombifolia* Vahl. (Vitaceae), *Melochia pyramidata* L. (Sterculiaceae), *Phyla strigulosa* Mart. and Gal., and the prostrate white verbena *Lippia nudiflora* L. (Verbenaceae), besides more abundant on an undetermined pink-flowered herb, also on *Boerhavia erecta* L. (Nyctaginaceae), and on *Eysenhardtia polystachya* Ortega.

The species *angulatus ammophiloides* Townsend has been found on flowers of *Lippiawrighti*. Nearctic eastern species have been found on *Helianthus* sp. In Mexico, at Milepost 1248, West Pacific Highway, the author and Marguerite Hull, the author's late wife, and son, Sillers Hull, took a large series of *Systropus* of two species on pink flowers of the coral vine *Corculum leptopus* (H & A) Stuntz. Robertson (1928) recorded *macer* Loew from the labiate *Pycnanthemum virginianum*, the verbeniates *Verbena hastata* and *V. urticifolia*, and the composites *Aster crocoides*, frequently on *Aster turbinellus*, *Bidens aristosa*, *Boltonia asterioides*,

Eupatorium serotinum, *Rudbeckia triloba*, *Solidago nemoralis*, and *Vernonia fasciculata*.

Bowden (1964) records 2 species of the genus in Ghana from the flowers of labiate *Hosundia opposita*.

Painter and Painter (1964) note that there is an even greater resemblance in these flies to wasp models during flight, such resemblance extending to such ichneumonids as *Therion* and *Thyredon*.

Distribution: Neartic: *Systropus ammophiloides* Townsend, 1901; *angulatus* Karsch, 1880; *arizonicus* Banks, 1909; *macer* Loew, 1863 [= *imbecillus* (Karsch), 1880 (as *Cephenus*), = *infuscatus* (Karsch), 1880 (as *Cephenus*)].

Neotropical: *Systropus acutus* Painter, 1963; *basilaris* Painter, 1963; *bicornis* Painter, 1963; *calopus* Bigot, 1892; *cerdo* Osten Sacken, 1887; *chilensis* Philippi, 1865; *columbianus* Karsch, 1880; *conopoides* Knuckel, 1904; *curranii* Carrera and d'Andretta, 1950; *dimidiatus* Curran, 1942; *dolorosus* Williston, 1901; *femoratus* (Karsch), 1880 (as *Cephenus*); *foenoides* Westwood in Guérin, 1842 [= *funereus* Costa, A., 1865]; *fumipennis* Westwood in Guérin, 1842 [= *niger* Walker, 1849]; *geijskesi* Curran, 1942; *lanei* Carrera and d'Andretta, 1950; *lugubris* Osten Sacken, 1887; *mars* Curran, 1942; *nigripes* Painter, 1963; *nitidus* Wiedemann, 1830 [= *brasiliensis* Macquart, 1847]; *oldroydi* Carrera and d'Andretta, 1950; *paloides* Painter, 1963; *pulcher* Williston, 1901; *quadripunctatus* Williston, 1901; *repertus* Carrera and d'Andretta, 1950; *rogersi* Osten Sacken, 1887; *rufiventris* Osten Sacken, 1887; *sallei* A. Costa, 1864; *semialbus* Painter, 1963; *similis* Williston, 1901; *vicinus* Painter, 1963; *willistoni* Curran, 1942; *xanthinus* Painter, 1963.

Palearctic: *Systropus acuminatus* (Enderlein), 1926 (as *Cephenius*); *annulatus* Engel, 1932; *barbiellinii* (Bezzi), 1905 (as *Cephenius*); *cantonensis* (Enderlein), 1926 (as *Cephenius*); *chinensis* (Bezzi), 1905 (as *Cephenius*); *divulsus* (Séguy), 1963 (as *Cephenius*); *excisus* (Enderlein), 1926 (as *Cephenius*); *exsuccus* (Séguy), 1963 (as *Cephenius*); *flavicornis* (Enderlein), 1926 (as *Cephenius*); *flavipectus* (Enderlein), 1926 (as *Cephenius*); *fodillus* (Séguy), 1963 (as *Cephenius*); *formosanus* (Enderlein), 1926 (as *Cephenius*); *gracilis* (Enderlein), 1926 (as *Cephenius*); *hoppe* Matsumura, 1916; *indogatus* (Séguy), 1963 (as *Cephenius*); *interlitus* (Séguy), 1963 (as *Cephenius*); *laqueatus* (Enderlein), 1926 (as *Cephenius*); *limbatus* (Enderlein), 1926 (as *Cephenius*); *maccus* (Enderlein), 1926 (as *Cephenius*); *melli* (Enderlein), 1926 (as *Cephenius*); *montivagus* (Séguy), 1963 (as *Cephenius*); *mucronatus* (Enderlein), 1926 (as *Cephenius*); *nigricaudus* (Brunetti), 1909 (as *Cephenius*); *nigritarsis* (Enderlein), 1926 (as *Cephenius*); *nitobei* Matsumura, 1916; *polistoides* (Westwood), 1876 (as *Cephenius*); *sauteri* (Enderlein), 1926 (as *Cephenius*); *sikkimensis* Enderlein, 1926 (as *Cephenius*); *studyi* (Enderlein), 1926 (as *Cephenius*); *submixtus* (Séguy), 1963 (as *Cephenius*); *suzukii* Matsumura, 1916.

Ethiopian: *Systropus atratus* Macquart, 1846; *barnardi* Hesse, 1938; *bicoloripennis* Hesse, 1963; *bicuspidis* Bezzi, 1924; *butneri* (Enderlein), 1926 (as *Cephenius*); *clavatus* Karsch, 1880; *crudelis* Westwood, 1876; *cuspidicauda* (Enderlein), 1930 (as *Symballa*); *diremptus* Enderlein, 1926; *fumosus* Hesse, 1938; *gracilis* Hesse, 1963; *hessei* François, 1954; *holaspis* Speiser, 1914; *ichneumoniformis* Hesse, 1958; *leptogaster* (Loew), 1860 (as *Symballa*); *limacodidarum* Enderlein, 1926; *macilentus* Wiedemann, 1828 [= *attenuatus* Macquart, = *capensis* Philippi, 1865, lapsus]; *marshalli* (Bezzi), 1924 (as *Diaerops*); *munroi* Hesse, 1938; *namequensis* Hesse, 1938; *quadripunctatus* Séguy, 1934; *rex* Curran, 1929; *rhodesianus* (Hesse), 1938 (as *Cephenius*); *rufidulus* Bowden, 1962; *ruffemur* (Enderlein), 1926; (as *Cephenius*); *rugosus* Bezzi, 1924; *sanguineus* Bezzi, 1921; *schineri* (Enderlein), 1926 (as *Coptopelma*); *sericeus* Bezzi, 1924; *sheppardi* Hesse, 1963; *silvestrii* Bezzi, 1914; *snowi* Adams, 1905; *subcingulatus* (Enderlein), 1926 (as *Cephenius*); *tenius* (Enderlein), 1926 (as *Cephenius*); *tessmanni* (Enderlein), 1926 (as *Dimelopelma*); *trigonalis* Bezzi, 1924; *vespiformis* (Enderlein), 1926 (as *Coptodierus*); *zuluensis* Hesse, 1938.

Systropus elegans is proposed as a new name for *Systropus quadripunctatus* Séguy (1934), preoccupied by Williston (1901).

Oriental: *Systropus blumei* Vollenhoven, 1863; *celebensis* Enderlein, 1926; *edwardsi* Brunetti, 1920; *eumenoides* (Westwood), 1842 (as *Cephenius*); *flavicoxa* (Enderlein), 1926 (as *Cephenius*); *furcatus* Enderlein, 1926; *numeratus* de Meijere, 1916; *ophioneus* (Westwood), 1849 (as *Cephenius*); *roepkei* de Meijere, 1914; *sphegoides* Walker, 1860; *tessellatus* Vollenhoven, 1863; *tipuloides* Westwood, 1876; *tricuspidis* (Enderlein), 1926 (as *Cephenius*); *udei* (Enderlein), 1926 (as *Cephenius*); *valdezi* Bezzi, 1917; *varipes* Edwards, 1919; *violacescens* (Enderlein), 1926 (as *Cephenius*).

Australian: *Systropus doddi* Roberts, 1929; *flavornatus* Roberts, 1929.

Genus *Dolichomyia* Wiedemann

FIGURES 93, 94, 335, 579, 589, 881, 882, 883

Dolichomyia Wiedemann, Aussereuropäische zweiflügelige Insekten, vol. 2, p. 642, 1830. Type of genus: *Dolichomyia nigra* Wiedemann, 1830, by monotypy.

Comparatively small flies with an extraordinary increase in the length of the slender abdomen and in the hind legs; in these respects they resemble *Systropus* differing from that genus in the much shorter antennae, the greater anteroposterior length of the head and in the absence of the axillary lobe on the wing. The wing is even more slender and lanceolate than in *Systropus* Wiedemann; the two genera are both bare and with relatively denuded appearance due to only minute pile, and both have a long, slender proboscis. The wings are glassy and hyaline.

This genus, except for the related new Australian genus *Zaclava*, is only known from the southwestern United States and Chile. Thus its present range is much more restricted than *Systropus* Wiedemann.

Length: 5 to 10 mm.

Head, lateral aspect: The head is large, almost entirely consisting of the eye, with very small, short, frontal triangle and smaller vertical triangle. The head is relatively long, nearly as long as high, the occiput in the male is shallow on the upper fifth of the head, dwindling away until none of it can be seen laterally. It is, however, more swollen and extensive on the lower part of the head. And this is true of both sexes. The pile of the occiput consists of pollen or minute pubescence with laterally along the middle a few, scattered, appressed, outwardly directed, short, bristly hairs against a black background and gray pollen. There is a sharp, vertical stripe of yellowish-white pollen running downward from the vertex and in the proper light most of the pollen on the lower part of the head is grayish white. The very small front is gray pollinose without pile. The face is very low and limited by the oragenal cup which extends close to the base of the antennae but which in profile is very short and linear. The pile consists of pollen or minute micropubescence only. The genae are linear.

The proboscis is quite long and slender. The labellum is equally slender and long and it constitutes more than one-third of the total length; it is sharply attenuate, the halves apposed; the whole proboscis is twice as long as the head and extends well beyond the antennae and is thrust straight forward. The palpus is extraordinarily slender but also very elongate and has 3 or 4 fine, oblique, dorsal, bristly hairs. It generally lies close against the proboscis and is not easily seen. The antennae are attached at the middle of the head, elongate and slender but much less so than in *Systropus* Wiedemann. The first segment is cylindrical, 3 or 4 times as long as wide, pale, pollinose, with a few, minute, oblique setae below. The second segment is widest apically and as long as its apical width, and about one-fourth as long as the first segment. The third segment is as long as the first two together, pollinose, the basal half a little thicker than the second segment and at this point narrowed to the blunt apex. The outer half of this segment is a little more than half as wide as the basal part. The whole antennae is perhaps not quite as long as the head.

Head, anterior aspect: The head is circular, the eyes extensively holoptic in the males. The head is much wider than the thorax, the antennae arise adjacent, the vertex is almost restricted to the ocellar tubercle, the latter is a little swollen. The relatively large ocelli lie on the eye margin. There is a narrow, vertical, pollinose wedge extended forward from the ocelli. The oragenal opening is large, elongate, oval, very deep with vertical sides but somewhat more slender on the upper fifth where it is divided by a triangular, sloping, medial ridge. It extends to within a short distance of the an-

tennae. Laterally the walls of the oragenal cup are quite narrow and also short and the upper lateral face and lower genae are linear. The tentorial fissure is deep but consists of a mere line with ventral pit. In a Chilean species the head is curiously long, and globular with the eye cut away on the dorsal half, leaving the occiput much exposed from above.

Thorax: The thorax is short and compact, somewhat similar to *Systropus* Wiedemann but with the metasternum less prominent and not forming fused or semi-fused, sclerotized, posterior plates, and also the mesonotum is higher and more convex, and is especially steep, vertically abrupt in front above the very short pronotum and curved inward and backward above the pronotum, to a somewhat greater extent than in *Systropus* Wiedemann. The humerus is outwardly swollen and rounded, elongate and extending obliquely backward. The mesonotum is either polished and bare, without a trace of pollen, but with moderately abundant, fine, erect pile or thinly pollinose and vittate with only a very few fine, short, erect hairs. The notopleuron forms a flat, flangelike ledge above the base of the wing somewhat as in *Systropus* Wiedemann but much less prominent.

The scutellum is small, convex with a few fine, short, stiff, erect hairs. The disc is pollinose even on those species which have a bare mesonotum; both halteres unusually large, with large, apical disc or club. The whole pleuron is pollinose and covered with dense, microscopically small, pollenlike scales; upper border of mesopleuron with a few long, stiff hairs appressed upward; remainder of pleuron without pile; squama quite short, without fringe of hairs but with some minute micropubescence. On each side at the base of the scutellum there is a small, circular, cuplike structure at the edge of the squama that corresponds to the strigula found on *Systropus* Wiedemann. There are 2 or 3 setate hairs below and behind the posterior spiracle.

In this genus the dorsal posterior extremity of the metasternum forms a distinct, inflated, rather long, dentate or sometimes bidentate flangelike, lateral extension. It probably corresponds to the small, embedded, oval, or triangular plate at the end of the metasternum situated dorsally in *Systropus* Wiedemann, which is also sometimes toothed.

Legs: Middle pair of legs about $1\frac{1}{2}$ times as long as the anterior pair and only about half as long as the hind pair, which, as in *Systropus* Wiedemann, are greatly lengthened. Beginning near the middle the hind femur is slightly swollen distally. The hind tibia is a little wider apically than at the base. In the new genus *Zaclava* the hind femur is very strongly clavate apically with a row of stout, sharp, ventral spines. The anterior tibia has 2 or 3 fine, short, oblique, bristly setae ventrally and also anterodorsally. The middle tibia has somewhat larger setae anterodorsally, dorsally and posteroventrally. The first 2 rows have about 3 setae, the last one about 7 setae. Hind tibia with prominent bristles, slender but not very long. They are principally

concentrated in a dorsal row and a posteroventral row, each containing about 10 elements. The pile of the tibiae consists of a few scattered setae hairs and some scattered, comparatively broad, appressed scales that are more abundant distally on each tibia, and more conspicuous on the hind pair. The anterior femur has a few fine, flat-appressed, scattered microsetae, and this femur is slightly enlarged and thickened in the middle and on the basal half; middle femur more slender with similar pile. The hind femur is narrow at the base, gradually widening until near the apex where it is nearly 3 times as wide. It has some broad, appressed scales, a few small, short, appressed setae bristles ventrally on the outer half and viewed in the proper light it appears to have microsetae arranged in transverse rows somewhat as in *Systropus* Wiedemann. The pulvilli are large and elongate with an empodium between. Claws sharp and slender.

Wings: The wings are hyaline, very slender and narrowed on the basal half due to the loss of the axillary lobe and the loss of the alula. There are only 3 posterior cells, each widely open, and the ambient vein is complete. The radial sector is quite short and there is a swelling of the vein where second and third veins meet. The anterior crossvein enters the discal cell close to but not quite at the outer third of that cell. In the type-species the anal vein is quite evident but is set quite far apart from the cubital vein. In the genus *Zaclava* the first anal vein is completely atrophied. There is a knob-like enlargement at the furcation of the second and third veins.

Abdomen: The abdomen in the type-species is 4 or 5 times as long as the thorax and of almost equal width apically as either in the middle or at the base, both when viewed from above and from the side. Thus the abdomen is subcylindrical, but is distinctly a little flattened and compressed laterally, more so at the end of each tergite and especially so upon the second to sixth segments. The posterior corners of each tergite have a more or less oval spot of silvery pollen. Pile of the abdomen minute, appressed and setate, the last tergite with a somewhat conspicuous fringe of bristly hairs apically. Apart from the hypopygium 8 tergites of nearly equal length are visible in the male and female, the eighth being a little shorter. Hypopygial elements above and below are of nearly equal length and apparently the tergite is inverted and reversed as in *Systropus* Wiedemann. The abdomen of the type-species extends far beyond the apex of the hind femur, but in the new genus *Zaclava* it extends only a very short distance beyond the apex of the femur and the abdomen is therefore comparatively shorter.

The male terminalia from dorsal aspect, epandrium removed, show a broadly widened structure toward the base, strongly and gradually narrowing apically with curious dististyli, which in lateral aspect are curved more or less like the letter C, blunt-lobed above and below. The epiphallus forms a broad, dorsal plate, more

or less triangular in aspect, occupying the entire outer half of the structure, arising narrowly from the ramus. In lateral aspect the epiphallus is prominent with a curious, attenuate, apical, downturned lobe, and the ejaculatory process has a narrow, prominent incision arising ventrally. The epandrium is triangular, the basistylus plane below, arched into a hemicycle above. None of the intricate accessory claspers are present, such as are so characteristic in *Systropus* Wiedemann. The relationship must be very distant.

Material studied: Several individuals of the type-species and one Chilean species.

Immature stages: Unknown.

Ecology and behavior of adults: In a personal communication Dr. Joseph Bequaert tells me that he collected individuals of the type-species on a species of *Solidago* at an elevation of 6,200 feet, in Mohave County, Arizona, on August 9. R. H. Painter has recorded collecting the same species on *Clematis* on August 23, west of Ft. Collins, Colorado.

Distribution: Nearctic: *Dolichomyia gracilis* Willis-ton, 1894.

Neotropical: *Dolichomyia decta* Schiner, 1868; *nigra* Wiedemann, 1830.

Zaclava, new genus

FIGURES 97, 333, 583

Type of genus: *Systropus clavifemoratus* Hardy, 1922, by present designation.

Differing from the type-species of *Dolichomyia* Wiedemann by the elongate, globular head in which the eye recedes forward leaving the occiput more exposed and with the hind femur strongly swollen on the outer half with numerous, stout, spinous bristles ventrally. The third antennal segment is flat, wide at the base and lanceolate and short. The anterior legs are quite short, proportionately much shorter than in *Dolichomyia* Wiedemann. Proboscis but little longer than the head, stout and robust, the broad, flattened labellum nearly as long as the proboscis. First anal vein completely atrophied.

These flies are known only from Australia.

Length: 5.5 to 10.5 mm.; more commonly 5 or 6 mm.

Material studied: Two new species collected in Australia.

Immature stages: Unknown.

Ecology and behavior of adults: The author collected two Australian species; one at the flowers of a blossoming tree of unknown genus some 10 or 15 miles from Melbourne late in December, and another at Lake George, New South Wales, on *Leptospermum* sp., earlier in that month.

Distribution: Australian: *Zaclava clavifemorata* (Hardy), 1922 (as *Systropus*); *minima* Roberts, 1929; *occidentis* Roberts, 1929.

Subfamily Xenoprosopinae Hesse, 1956

In 1956 Hesse described a very peculiar and aberrant bombyliid from South Africa for which he erected a new subfamily.

A very strange fly immediately distinguished by the large pendulous lobe attached below to the first antennal segment and the greatly reduced mouthparts and lobe-like palpi.

This medium-size fly has, in addition, relatively short legs, no bristles on the body, and no spines on the femora. The short pulvilli are almost spinelike. Blackish in ground color, with fine, white, scaliform pile on the yellowish postmargins of the abdominal tergites. Hesse (1956) notes that it has somewhat the appearance of an asilid or therevid as it rests upon the sand. Wing reduced in size. The wing venation, which is distinctly generalized, shows some relationship to the tribe Cythereini; it is worth noting that the only other bombyliid genera with vestigial mouthparts, *Villoestrus* Paramonov, *Oestranthrax* Bezzi, and *Marleyimyia* Hesse, all belong to the Exoprosopinae to which the Cythereini show a measure of transitional relationship, but which may be only parallel development. The genus *Xenoprosopa* Hesse is even more aberrant. It is known only from a single female, and until males are available I leave it in the new subfamily created for it by Hesse (1956).

Genus *Xenoprosopa* Hesse

FIGURES 84, 339, 539, 760

Xenoprosopa Hesse, Ann. South African Mus., vol. 35, p. 942, 1956. Type of genus: *Xenoprosopa paradoxa* Hesse, 1956, by original designation.

A very strange fly immediately distinguished by the large pendulous lobe attached below to the first antennal segment and the greatly reduced mouthparts and lobe-like palpi.

This medium-size fly has, in addition, relatively short legs, no bristles on the body, and no spines on the femora. The short pulvilli are almost spinelike. Blackish in ground color, with fine, white scaliform pile on the yellowish postmargins of the abdominal tergites. Hesse (1956) notes that it has somewhat the appearance of an asilid or therevid as it rests upon the sand. Wing reduced in size. The wing venation, which is distinctly generalized, shows some relationship to the tribe Cythereini; it is worth noting that the only other bombyliid genera with vestigial mouthparts, *Villoestrus* Paramonov, *Oestranthrax* Bezzi, and *Marleyimyia* Hesse, all belong to the Exoprosopinae to which the Cythereini show a measure of transitional relationship. This genus

Xenoprosopa Hesse is even more aberrant. It is known only from a single female, and until males are available I leave it in the new subfamily created for it by Hesse (1956).

These are peculiar and remarkable flies. The most unique feature is the odd antenna coupled with the peculiar oral structure. The proboscis and palpus are much modified, reduced, and transformed and the face depressed. Antennae set close together, with fine hairs on all segments. The first segment has a large, pendulous, prominent, conspicuous, densely haired, inflated, lobelike extension below the segment.

The occiput is rather short, only slightly concave behind, with a distinct, broad, shallow, central, groove-like depression, extending down from behind the ocellar tubercle, and bounded on each side just behind the dorso-posterior angle of the eyes with a slight, but distinct, prominence or lobe.

Hesse (1965) believes that this genus is nearest the Cythereini and that it shows some relationship, though slight, to *Oniromyia* Bezzi.

These flies are readily recognized, Hesse states, by the whitish hair, conspicuous, yellow-ringed abdomen, and yellow legs. They are known from a single female from Pofadder, Bushmanland, taken in October.

Known only from Bushmanland, South Africa.

Length: 10 mm.; wing 7 mm.

As I have not been able to see or obtain material of *Xenoprosopa* Hesse, I quote the author's description of this genus. Hesse states:

Body somewhat elongate. Head broader than thorax, much broader than long; occiput relatively short, only slightly concave behind, but with a distinct, broad and shallow, central, groove-like depression, extending down from behind ocellar tubercle and bounded on each side just behind dorso-posterior angles of eyes by a slight, but distinct, tumid prominence (or lobe); hind margin of eyes only slightly sinuous, not deeply indented and without a bisecting line; ocellar tubercle broad, only slightly raised, its postero-lateral ocellus on each side well developed, slightly elongate, much larger than small anterior and medial one; frons markedly broad, equally broad throughout, slightly and broadly depressed in front of ocellar tubercle, somewhat transversely prominent a little behind antennae.

The antennae are somewhat close together and with fine hairs on all the joints; joint 1 with a large, prominent and conspicuous, fairly densely haired, inflated or lobe-like extension below; joint 2 transverse, its outer apical angle somewhat sharply pointed; joint 3 stoutish, broadened basally, clubshaped, ending apically in a small or short terminal joint, itself ending in a slender stylet; facial part in front (or below) antennae slightly depressed or excavate, showing and lodging the following mouthparts and structures: a transverse groove demarcating anterior margin of actual face, a central raised boss-like part, separated from eyes and genal part by a deep sulcation or groove (genal groove) and ending medially and anteriorly in a downwardly projecting, somewhat triangular and bluntly

pointed process or spine (? anterior or reduced rim of modified buccal cavity) which is bounded on each side and below or behind it by an oval, inflated, hair-covered lobe (? modified palps), these mouthparts in turn being bounded behind by a downwardly projecting lip-like process or extension (? posterior rim of modified buccal cavity). Thorax shortish, subquadrate, but longer than broad, slightly convex anteriorly, appearing slightly humped; scutellum relatively smaller than in other Bombyliid genera, narrowish, rather tumid, leaving on its sides much of postalar calli exposed.

The legs are short, relatively feebly developed, without any spines on femora, only with fine and short hairs, the middle ones however with longish fine ones on outer face; tibia with the front and middle ones scarcely or only a little shorter than femora, the hind ones much shorter, covered with numerous very short spicules, in more than four rows; apical spurs of tibiae short, relatively feebly developed; tarsi shortish, shorter than tibiae, slightly compressed in apical part, especially hind ones, with relatively feebly developed, short spicules, the front tarsi not modified or different from the others; pulvilli present. Vestiture on body relatively poorly developed, composed of fine, shortish, hairs and fine hair-like scales, the former densest on head and the latter on abdomen, without any stiffer bristly hairs or bristles on any part of body; hairs on abdomen, even on sides, fine and very short, absent on venter; pteropleuron, hypopleuron

and greater part of metapleuron bare; plumula entirely absent; scaling on legs fine.

The wings are relatively short and narrowish; membrane wrinkled; basal comb wanting; alula wanting; second vein originating some distance before middle cross vein; only two submarginal cells present; discoidal cell relatively short; four posterior cells present, of which the first and third are narrowed apically, the third being very characteristically triangular in shape; anal cell elongate, narrowish; squamae triangular, sparsely hairy along hind border; knobs of halteres rather large. Abdomen elongate, with 7 visible segments in female and in this sex with a posterior genital tuft.

Material available for study: None. This genus is known only from the unique type.

Immature stages: Unknown.

Ecology and behavior of adults: Hesse (1956) states that this unique and remarkable fly has some resemblance to an asilid or therevid when resting upon the sand.

Distribution: Ethiopian: *Xenoprosopa paradoxa* Hesse, 1956.

Subfamily Platypyginae Verrall, 1909

These small anthophilous flies have a characteristic habitus because of their strong humped mesonotum and the globular head. The proboscis while of no great length is usually as long as the head, yet it extends well beyond the confines of the oral cavity and in some species it may be much longer than the head. In the first of two groups the discal cell is complete, as in *Platypygus* Loew, and in the second group the discal cell is open due to the absence of the crossvein; in this second group are found *Cyrtosia* Perris, and also *Onchopelma* Hesse in which the anal cell is closed and stalked, besides the curious Australian genus *Cyrtomorpha* White.

In *Cyrtomorpha* White the size is a trifle larger, the flies have a very compact, subglobular abdomen and the larvae feed within the egg pods of locusts. This is the only genus in the subfamily where we have any knowledge of the larval habits or hosts. The second vein ends

close to the first and the proboscis is shorter than the head.

The subfamily *Platypyginae* is characterized and separated from the *Mythicomyiinae* by the presence of a distinct, well-developed second vein ending independently in the costa beyond the first vein and also by the unbranched third vein. There are present 4 posterior cells, the anal cell usually open, except *Onchopelma* Hesse, and the alula absent or very much reduced.

In *Cyrtisiopsis* Séguy, a genus extending into South Africa, the posterior ventral part of the head is curiously drawn-out and extended backward; probably all those species of *Platypygus* Loew with extraordinarily extensive postocciput should be placed in *Cyrtisiopsis* Séguy. *Ceratolaemus* Hesse though lacking a discal cell also has a remarkable postocciput, raising the question of the comparative value of the discal cell as contrasted with occipital structures. Hesse (1938) calls attention



TEXT-FIGURE 36.—Pattern of the approximate world distribution of the species of the subfamily Platypyginae.

to the adaptation of this subfamily and flies of the genera *Apolysis* Loew and *Phthiria* Meigen to the matter of floral adaptation. This subfamily has been found on all continents, except South America, and it probably occurs there. These flies seem especially well developed in the Mediterranean and South Africa and probably many more species and unique types are to be found below the equator.

In this subfamily belongs the remarkable genus *Psiloderoides* Hesse. These flies for which I erect the tribe Psiloderini are much like acrocerid spider parasites in general appearance. They are unique also in the marked reduction of the proboscis. They are nearest to

the Australian genus *Cyrtomorpha* White in which the proboscis though short is still present, but the discal cell is wanting. Both genera live in and destroy egg pods of locusts.

The subfamily Platypyginae is a disparate group, containing as it does such curious flies as *Psiloderoides* Hesse and *Cyrtomorpha* White.

Those genera with the discal cell absent I include in the tribe Cyrtosiini, including *Ceratolaemus* Hesse, with its quadriarticulate antenna. *Platypygus* Loew and *Cyrtisopsis* Séguin I would place in the tribe Platypygini.

KEY TO THE GENERA OF PLATYPYGINAE

1. The discal cell is complete, with 3 veins leading from it . . . 2
The discal cell is open, the posterior crossvein absent, consequently the second posterior cell has a long petiole. The anterior limb of the fourth vein has 2 branches, which may sometimes be faint 4
2. Proboscis reduced to a minute, nipplelike structure. Habitus like that of acrocerids; mesonotum humped and abdomen wide, inflated, decumbent. Almost bare flies.
Psiloderoides Hesse
Proboscis clearly present 3
3. A remarkable gular process present on the postventral part of the much extended occiput. Proboscis much longer than the head. The third antennal segment has only a small microsegment *Cyrtisopsis* Séguin
No drawn-out gular process even if postocciput is extensive and well developed. Proboscis as long as head or shorter.
Platypygus Loew
4. The anal cell is closed with a long stalk or petiole. The anal vein and distal branches of the fourth vein may be faint or evanescent. The third antennal segment has a prominent extra distal segment so that the antenna are quadriarticulate. Hind basitarsus of males at least in type-species with curious pronglike process. Third vein extraordinarily

- straight. Second vein ends close to first vein; male eyes in contact *Onchopeltina* Hesse
The anal cell is open, at most closed in the margin. Axillary lobe narrow 5
5. Head distinctly elongate due to the remarkable lengthening of the occiput posteriorly which is produced directly backward as a curious spinelike ventral process. Eyes widely separated in both sexes with a minute kink in the margin behind antennal insertion. Antenna also quadriarticulate.
Ceratolaemus Hesse
Head rather spherical or slightly oval. If the occiput is prominent posteriorly it is not produced ventrally into any process or spine 6
 6. The second vein ends much closer to the first vein than to the third vein. The anterior crossvein lies at or beyond the middle of the wing. The proboscis is stout and much shorter than the head. The third antennal segment is wide basally, narrowed apically. Compact flies of 2 to 5 mm. length with compact, wide, subglobose, semidecumbent abdomen *Cyrtomorpha* White
The second vein ends midway or nearer to the third vein. Proboscis as long as the head or longer. Plump, hump-backed flies with longer, stout, robust abdomen. Third antennal segment elongate ovate *Cyrtosia* Perris

Genus *Cyrtosia* Perris

FIGURES 321, 593

Cyrtosia Perris, Ann. Soc. Ent. France, vol. 8, p. 55, 1839. Type of genus: *Cyrtosia marginata* Perris, 1839. [Bezzi p. 3, 1924 gives *C. marginata* type-species.]

Cyrtosia Rondani, Arch. Zool. Anat. Fisiol., vol. 3, (sep.) p. 73, 1863, lapsus.

Cephalodromia Becker, Ann. Soc. Ent., Paris, vol. 83, p. 121, 1914a. Type of genus: *Cephalodromia curvata* Becker, 1914, by monotypy (as an empidid).

Engel (1933), pp. 105-106, key to 21 Palaearctic species and sub-species.

Efllatoun (1945), pp. 36-37, key to 9 species from Egypt.

Flies of *Cyrtosia* Perris are always small, often minute, and are readily characterized by the strongly humpbacked mesonotum, the quite bare aspect, the strongly developed occiput, which Efllatoun (1945) calls puffed out, and the prominent pronotum and metanotum. They are usually yellowish flies with conspicuous vittate pattern of blackish or brownish coloration

on thorax and fasciate pattern upon the abdomen. The radial sector is forked with the second vein well developed and ending beyond the first vein; this separates *Cyrtosia* Loew and related genera from the subfamily Mythicomyiinae. The third vein has only one branch.

On the wing, which is hyaline, the alula is absent, the axillary lobe well developed but less so than in Mythicomyiinae; the auxiliary vein or subcosta is evanescent, fading away at the apical end. It is important to note that the discal cell is absent and the anterior crossvein is farther from the base of the wing so that the first basal cell is longer than the second. The anal cell is widely open.

The pleuron is high and higher even than the hump of the mesonotum and the head is attached lower than in Mythicomyiinae. The head is apt to be shriveled. The third segment is pyriform or ovate with a short, thick, microscopically pubescent style.

The flies of this genus are found principally along the Mediterranean Coast, in Spain, Sardinia, Asia Minor, Turkestan, etc., and Efllatoun noted 10 species from

TEXT-FIGURE 37.—Habitus, *Cyrtosia nitens* Loew.

Egypt. Hesse has described 2 species from South Africa.

Melander described a species of the related genus *Platypygus* Loew from the southwestern United States. So far the subfamily Mythicomyiinae has a much wider world distribution.

Length: Commonly 1.5 mm., or 2.5 mm., but reaching 4.6 mm. in a few species.

My description taken from the flies in the British Museum (Natural History) has been supplemented by Efflatoun's very excellent description.

Head: Usually ovoid, sometimes as long as, or longer than, broad, and often narrower than the thorax; occiput considerably puffed out and conspicuously produced below, ventrally behind the opening of the mouth, into a triangular or conical projection, which is best seen in profile; frons broader above near the vertex than below where it is always more or less deeply excavated (in most specimens owing to shriveling when dried) and when viewed in profile its sides form almost an angle of 45 degrees with the face which is quite as long (as the frons) and, as in *Empidideicus*, usually more or less produced above, at the upper margin of the mouth; eyes, as in the two preceding genera, with the facets of equal size all over and widely separated in both sexes; genae very narrow, linear; proboscis varying considerably in length, from shorter than the head to as long as

the length of the head and the thorax together, in fact it often varies so much in individuals of the same species that it cannot afford a reliable character of distinction; palpi apparently absent, or if present then only very minute and rudimentary (as an extremely minute, microscopic projection bearing a few hairs at the apex); vertex broad, with the ocelli placed on a very feebly raised ocellar tubercle or almost on the same level as the sides of the vertex and the ocelli always form a fairly wide triangle owing to the median ocellus being always placed a little in front of the lateral ocelli.

Antennae inserted about halfway between the vertex and the upper margin of the mouth and consist of a short cylindrical basal segment, a very short somewhat broader second segment and a pyriform to elongate-ovate third segment ending in a short but usually thick style (the thickness due to dense microscopic pubescence); this style, as a rule, is distinctly shorter than in the preceding genus.

Thorax: Very much humpbacked, distinctly more so than in *Leylaiya* and in *Empidideicus*, and with the pronotum and metanotum well developed; the attachment of the head to the thorax is distinctly lower than in the two preceding genera, being much lower than the notopleural suture; humeral and postalar calli stronger than in *Empidideicus*; pleuron well developed and its height usually exceeds the hump of the mesonotum, above the notopleural suture.

Wings: Wings with the alula absent but the anal lobe well developed and with the venation less reduced than in the two preceding genera:

The Sc fades away in the cell, before reaching the costa and the latter is strong and thickened a little beyond the tip of vein R_{4+5} ; the radial sector consists of 2 branches, R_{2+3} and R_{4+5} , in addition to the short upper branch R_1 , which joins the costa well after the middle; the r-m crossvein is placed further away from the base of the wing than in the other two preceding genera, i.e., toward the middle; the basal portion of vein M_{1+2} , which forms the upper margin of cell 2nd M is usually less strong than the anterior branched fork and 1st M_2 cell is always absent; vein 2nd A is well marked almost to the wing margin, consequently cell 1st A is present and is always more or less widely open; squamae small, with a very sparse, delicate fringe; halteres comparatively short, with a very large knob.

Legs: Moderately long and strong; front and hind coxae long; tarsi, especially the metatarsi, are somewhat long and the apical tarsal segments are usually blackish, partly due to the black pubescence on these parts only; claws and pulvilli small.

Abdomen: Usually not broader than the thorax, cylindrical, feebly bent downward, and often somewhat dorsoventrally flattened; it consists of 7 or 8 segments and the genitalia in both sexes are almost always entirely concealed; the pubescence although sparse and very short is usually distinct.

Material available for study: The series in the collections of the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Efflatoun (1945) notes that the flies of this genus are usually captured

only on or in flower heads; he found them in large numbers in desert Compositae as well as flowers of the common desert plant *Zilla spinosa*. He found hundreds of individuals of *marginata* Perris in February and March on flowers of *Calendula* and *Chrysanthemum*.

Distribution: Palaearctic: *Cyrtosia abragi* Efllatoun, 1945; *aglota* Séguy, 1930; *annicola* Bowden, 1965; *bicolor* Abreu, 1933; *canariensis* Engel, 1932, *canariensis tenuis* Frey, 1958; *cinerascens* Loew, 1873; *cognata* Engel, 1933, *cognata trisignata* Engel, 1933; *crocea* Séguy, 1949; *flavorufa* Strobl, 1909; *fusca* Séguy, 1938; *gulperii* Efllatoun, 1945; *humeralis* Abreu, 1933; *injii* Efllatoun, 1945; *jeanneli* Séguy, 1949; *luteiventris* Bezzi, 1926, *luteiventris minima* Efllatoun, 1945; *marginata* Perris, 1839; *meridionalis* Rondani, 1864; *nitens* Loew, 1846; *nitidissima* Engel, 1933; *nubila* Bezzi, 1925; *obscura* Fabricius, 1904; *obscuripes* Loew, 1855, *obscuripes maculithorax* Engel, 1933, *obscuripes serena* Becker, 1915; *occidentalis* Rondani, 1863; *opaca* Loew, 1846; *pallipes*, A. Costa, 1885; *perfecta* Becker, 1910; *persicana* Becker, 1903; *pusilla* Loew, 1873; *seia* Séguy, 1963; *separata* Efllatoun, 1945; *tetragramma* Bezzi, 1926, *tetragramma canariensis* Engel, 1933.

Ethiopian: *Cyrtosia curvata* Becker, 1914; *fusca* Séguy, 1938; *ornatifrons* Séguy, 1932; *namaquensis* Hesse, 1967; *stuckenbergi* Hesse, 1967.

Australian: *Cyrtosia parvissima* Roberts, 1929.

Genus *Ceratolaemus* Hesse

FIGURES 334, 585, 592

Ceratolaemus Hesse, Ann. South African Mus., vol. 34, p. 969, 1938. Type of genus: *Platypygus* (*Ceratolaemus*) *xanthogrammus* Hesse, 1938, as a subgenus, by original designation.

Ceratolaemus Hesse is distinguished from its nearest relatives by the lack of the discal cell. It is my belief that it should be put in a separate genus.

These flies are known only from South Africa, and like other members of the Cyrtosiniinae they frequent blooms of various flowers in which they may be found feeding.

Length: Of body, about 2¼-2½ mm.; of wing: about 2½-3 mm.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of male with basal parts; the apical process in form of a bidentate structure; aedeagal complex with the aedeagus distinct and slender and joined on to basal parts by a ramus on each side; the basal strut and parts by a ramus on each side; the basal strut and lateral struts cannot be distinctly made out and are minute in contrast with the same structures in *Onchopelma* and *Empididicus*; the basally directed rod on each side is, however, distinct.

Material available for study: My illustrations are taken from the material of the British Museum (Natural History). I was unable to obtain a dissection of the genitalia.

Immature stages: Unknown.

Ecology and behavior of adults: Unknown.

Distribution: Ethiopian: *Ceratolaemus bilineatus* Hesse, 1967; *longirostris* Hesse, 1967; *montanus* Hesse, 1967; *xanthogrammus* Hesse, 1938.

Genus *Onchopelma* Hesse

FIGURES 352, 538, 580, 582, 590

Onchopelma Hesse, Ann. South African Mus., vol. 34, p. 973, 1938. Type of genus: *Onchopelma pulchellum* Hesse, 1938, by original designation.

Quite small flies; in females there is a superficial appearance to some females of *Heterotropus* Loew and *Phthiria* Meigen which is occasioned by the similar size and yellow color but with radically different wing venation and antenna. The hind basitarsus of males shows a curious, conspicuous, basal hook. The abdomen is plump rather than slender and the mesonotum less strongly humped than in other members of the Cyrtosiniinae. The head is subglobular, the male eyes in contact, the occiput short, flattened, normal. The palpus is small, the proboscis shorter, stouter than in *Platypygus* Loew and the labellum longer and better developed. The first basal cell is considerably shorter than the second due to the extreme basal position of the anterior cross-vein; the marginal cell is present but there is only a single submarginal cell, and while there are 4 posterior cells there is no discal cell. The auxiliary vein is evanescent distally, and while the first, second, and third veins are strong, the branches of the medius and cubitus are very weak, especially as they approach the wing margin; Hesse (1938) shows the second anal vein as evanescent; my figures from types show it strong, but the anal cell is closed with a quite long stalk. The base of the wing is quite broad in contrast to *Cyrtosia* Perris, due to a very broad axillary lobe; in spite of this the alula is much narrowed or absent. Finally, there is no transverse depression on the front as in *Phthiria* Meigen; front very small in males, broad and wide in females. Curiously the antenna is 4-segmented, the third segment bearing a second segment, as wide as the first, at least half as long, and with small attached stylelike microsegment.

These flies are known only from 3 South African species.

Length: 3 to 3.5 mm.; wing 3 to 3.5 mm.

Head, lateral aspect: Shining yellow flies. The head is distinctly subglobular, the frons, face, and gena bare or nearly so. All pile on these insects very fine, soft, rather sparse. The face is angularly produced forward but only to a very moderate extent. The antennae are attached at or very close to the middle of the head. The occiput is more prominent and tumid and extensive in females; in males it disappears in profile toward the vertex, and without a conspicuously developed central cavity; occipital pile fine, sparse, setiform. The ocellar tubercle, however, large, broad, and conspicuous. The

posterior eye margin is slightly but distinctly convex, becoming more so above and below. The palpus is small, not easily discovered, and tucked away hidden in the basal sheath of the proboscis. The proboscis is stout, robust, never longer than the head, and the labellum is prominent and has small spinules, or erect, downturned, stiff bristles. The antennae are rather large, somewhat swollen in *trilineatum* Hesse, more slender in *pulchellum* Hesse; the first and second segments are nearly equal and bear scattered appressed setae; the combined third and fourth segments vary from about twice as long as the first two segments to somewhat less long; the entire length of the antenna is equal the length of the eye; the fourth segment bears a minute spine, or microsegment at the apex.

Head, anterior aspect: The head is nearly the same width as the thorax. The front is broad in females, very small indeed in males; the female front has only a faint indication of a central, vertical depression. The upper eye facets of males are distinctly but not conspicuously larger. The oragenal opening or recess is deep and broad with the upper edge rectangular. The quite large ocelli are situated in a triangle with strong, raised tubercle; in males they rest upon the eye margin. The antennae are attached adjacent.

Thorax: Rounded and convex, less humped than in *Cyrtosia* Perris. The scutellum is transverse. The squamae are small, greatly reduced; halteres short, knobs subglobular or oval.

Legs: The legs are comparatively stout and rather short; there are no spines or bristles beneath the femora. The tibiae are distinctly short and not even the tibia longer than the femur; they have only short, spiny hairs below; there are short apical spurs and the hind basitarsus in males has a curious, conspicuous, curved, slender, bristle-tipped spur, or hooklike process; this process has a single, long, spinelike bristle projected upward. The claws and pulvilli are well developed.

Wings: The wings are hyaline. There is a marginal cell but only a single submarginal cell. While there are 4 posterior cells there is no discal cell. The anterior crossvein is far backward toward the base of the wing, placed barely beyond base of second vein. The auxiliary vein is evanescent and so are all the branches of medius, cubitus, anal veins, etc., which normally reach the wing margin. The wing is unusually broad at base but the alula is vestigial or absent.

Abdomen: There are 7 visible segments in the male and 8 in the female. Most of the male hypopygium is exposed; the upper apical angle of the terminal male sternite is angularly and sharply produced. The male hypopygium has distinct bristly hairs basally; according to Hesse (1938) the basimeres are connected to the aedeagal structures by the prolonged basal part; there are apical processes that correspond to the dististyli (beaked apical segments) of the Bombyliinae; they are lobelike and have a stout hook ventrally at the base. As to aedeagal structure, the aedeagus is slender; there is a slender, basally directed rod on each side and a

ventrally directed curved rod on each side; lateral struts are well developed; the basal strut has no lateral process on each side, it is very broad, with a flattened laterally extended flange attached dorsally on each side.

Material available for study: The types of both known species in the British Museum (Natural History), from which Arthur Smith made the accompanying illustrations.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Onchopelma karoanum* Hesse, 1967; *pulchellum* Hesse, 1938; *trilineatum* Hesse, 1938.

Genus *Psiloderoides* Hesse

FIGURE 340

Psiloderoides Hesse, Ann. South African Mus., vol. 50, part 6, p. 121, 1967. Type of genus: *Psiloderoides mansfieldi* Hesse, by original designation.

Very curious flies that greatly resemble small acrocerids. These are small flies of only a few millimeters length. It is rather readily recognized by the minute, nipplelike, or fingerlike lobe representing the much reduced proboscis. The antennae are comparatively short, all segments of about the same length; the third segment has a very thick style, or microsegment with a bristle at tip.

These flies, however, are noteworthy for their strong resemblance to the spider parasitic flies: the abdomen is large, swollen, much decumbent, and subglobular and it is considerably wider than the thorax. The mesonotum is greatly humped and the small head decumbent to a marked degree. Upon the hyaline wing the marginal cell is shortened and there is only 1 submarginal cell. While there are no bristles present the pile of the vestiture is better developed than in related flies. The legs are rather small, a trifle swollen or thickened upon the femora.

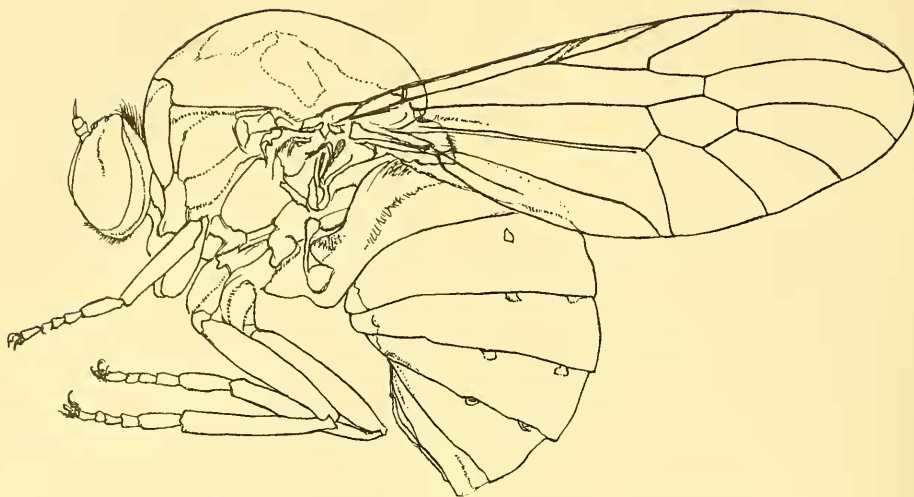
These flies have 4 posterior cells and a well-developed discal cell of small, rather wide, and short proportions. They are possibly related to the Australian *Cyrtomorphia* White, which is also subglobose and more or less resembles an acrocerid and, like *Psiloderoides* Hesse, is also a consumer of locust-egg packets in larval stages.

These flies were taken in the Kenhardt District of South Africa in May.

Length: 2.6 to 3.2 mm.; of females 4.2 to 4.4 mm.; of wings 3.2 to 3.88 mm.; of females 4.36 to 4.96 mm.; width of female abdomen, up to 3.6 mm.

Just as the present work was ready to be submitted for publication I was in receipt of Dr. Hesse's paper describing 3 remarkable new genera of bee flies from South Africa. I quote this description:

This new genus, of which the known representative have a striking resemblance to species of the genus *Psilodera* of the spider parasites (dipterous family Acroceridae), is established



TEXT-FIGURE 38.—Habitus, *Psiloderoides mansfieldi* Hesse. Redrawn after Hesse.

to accommodate a remarkable bombyliid submitted by Mr. R. J. Mansfield and of which the adults were reared in a laboratory of the Department of Agriculture in Pretoria from a batch of bombyliid larvae found both in egg-packets of the brown trek locust (*Locustana pardalina*) and in loose soil in association with such egg-packets.

This bombyliid cannot be referred to any other subfamily of the Bombyliidae but to the Cyrtosinae [renamed Platypyginae]. With the latter it agrees in certain characters, such as the reduction of the wing-venation, the presence of only one submarginal cell, the peculiar reduced and somewhat triangular marginal cell, the characteristic quadri-articulate antennae, the slight indentation in the inner margin of the eye opposite the antennae, the absence of distinct spines and spicules on the legs, absence of macrochaetae on body, the arched or humped and convex thorax, broad and arched abdomen, and rows of small shiny depressed black spots on abdomen (present in some cyrtosines [platypygines]).

In certain other characters, such as the very much reduced, rudimentary or vestigial proboscis, the widely separated ocelli of which the middle, slightly anterior, one is remarkably large, the less developed occiput, the sculptured or punctured thorax and abdomen, the excavate venter, and even more convexly humped or arched thorax and abdomen. It, however, differs from other known genera of the Cyrtosinae [Platypyginae] to such an extent that at least a distinct section or tribe of the latter is indicated to include it.

As the life histories of all the other known South African cyrtosine [platypygine] bombyliids (if not of the world) are unknown, the discovery of this genus and its host is of great importance.

The genus is characterized as follows:

Body arched and humped, with a striking and marked resemblance to that of the genera *Psilodera*, *Terphis* and *Thyllis* of the spider parasites (fam. Acroceridae), its widest part across between tergites 2 and 3.

Head almost spherical; occiput more flattened, not very prominent, more like that of *Onchopoma*, medially not depressed behind ocellar prominence; eyes large, not tending to be situated far forwards, separated on vertex in both sexes, apparently

more widely so in females their inner margin slightly indented opposite antennae, in females somewhat uneven, not uniformly convex, but slightly shallowly depressed groove-like from ocellar corner obliquely down to near middle; ocellar prominence relatively broad, slightly more raised in males, transverse, delimited from frons by a distinct, forwardly-curved, depressed line or suture, not evident in other cyrtosine genera, the lateral ocellar part higher than middle. The ocelli are widely separated, more so than in the other genera, in a slightly forwardly-curved line, the lateral ones very near or at upper corner of eyes and thus very broadly separated, the ocelli relatively large, especially the middle one which is also more elongated transversely; frons with a slight central depressed line, slightly raised on each side basally in front of each lateral ocellus, broader in females, broader basally than at antennae, and slightly broader than long; face in side view curving down to buccal cavity to the same extent as eyes, longer and narrower than frons, basally separated from antennal insertions by a transverse depression or depressed line, slightly narrowing from base to apex (beginning of buccal cavity); buccal cavity gradually widening to head below, the interocular space on head below being as wide as, or slightly wider than, base of face, the buccal depression not very deep, as long as, or slightly longer than, face; proboscis much reduced, minute or vestigial, represented by a small finger-like lobe or minute nipple; antennae situated close together, quadri-articulate, joint 4 elongate, slender, rod-like, narrower than rest, armed with a terminal style or short bristle, joint 2 cup-shaped; head below and behind broadish, slightly depressed, not sulcate.

Thorax almost globular, very convex above, in side view semi-circularly arched or humped above and high above level of vertex, almost or about as high above latter as depth of head itself; anterior sloping part behind head very steep, slightly hollowed and prothoracic part not distinctly separately discernible or prominent as in genus *Cyrtosia*; prothoracic humeral lobes broad, rounded, reminiscent of those of the Acroceridae; sides of thorax above notopleural fold a little anterior to wings not distinctly transversely depressed as in the other genera; postalar calli, owing to convexity of thorax, not so prominently ridge-like; dorsum or discal part of thorax above aerolately

punctured, more rugulose posteriorly; scutellum relatively broad, with a slight, but distinct, arcuate depression across basal part; pleurae slightly more convex or bulging than in the other genera, the mesopleuron more triangular and with some setiferous puncturation.

Wings either clear as in males or slightly infuscated as in females; marginal cell reduced, the posterior vein of which joins the costal margin much before apex of wings; one submarginal, a discoidal and four posterior cells present; first basal cell longer than second; anal cell open apically; axillary lobe narrowish, not lobe-like; alula much reduced, narrowish and linear; knobs of halteres tetrahedral in shape.

Abdomen broad, ovate, at broadest part (between tergites 2 and 3), much broader than thorax, arched or humped in appearance; discal part of tergite 1 flattened, slightly depressed, aerolately punctured; rest of tergites above in females also aerolately punctured or sculptured, but only discal basal three-quarters of tergite 2 and to a certain extent narrow discal basal part of 3 (under apical margin of 2) in males, in addition to flattened discal part of 1, aerolately sculptured; rest of tergites in males very finely transversely rugulose sculptured; dorsum of abdomen in both sexes with two rows of segmental, slightly depressed, shiny, dark or blackish spots on each side from tergite 2 to apex as in some other Cyrtosiniinae [Platypyginae], each spot nearer base of the tergite, and in some males often also with an extra central part of tergite 2; venter markedly and characteristically hollowed or excavated, the sides of tergites and plate-like hinder part of metapleurae much inflexed and overhanging venter, and middle of venter with two longitudinal ridge-like elevations.

Legs relatively stoutish and shortish, without any spines on hind femora and without distinct spicules on tibiae; apex of tibiae without distinct spurs, but apparently ending in a minute spine-like point on each side of tarsal insertion.

Vestiture without any macrochaetal elements, the hairs distinctly more developed than in other genera, excepting *Onchopelma*, even the hairs in females, though much shorter than in males, still denser and more evident than in most cyrtosine genera; hairs on thorax above, scutellum and mesopleuron situated in the areolar crater-like punctures, comparatively dense, longer in males than in females, in latter however apparently equally dense; those on abdomen, sides of tergite 1, greater part of 2 and on rest of tergites in males, though shorter than on thorax, markedly dense, shining silvery whitish, arranged transversely and directed towards centre along the middorsal line of which they form a sort of ridge composed of hairs; hairs on abdomen above in females situated in the crater-like punctures, very much shorter than in males, minute, but also directed towards midline; posterior and lower parts of pleurae bare; hairs on legs relatively longer and denser than in the other genera, slightly longer and finer in males than in females.

Hypopygium of males with the last sternite not spined or very sharply produced at its posterior apical angle as in most other cyrtosine genera; the basimere of the paramere rather broadish, more saddle-shaped, not shell-like as in the other genera; the telomeres of paramere leaf-shaped, flattened, without any hook or hook-like structure; aedeagal apparatus with the aedeagus proper appearing double at its end, reversed in position, bending towards dorsum instead of towards venter or downwards as in most bombyliids; posterior end of the apodeme of the aedeagal apparatus bulb-like or vesicular, not flattened as in most bombyliid genera; and the paraphyses of the apparatus in form of a ventral hood-like extension of which the hind margin is slightly emarginate medially.

Material available for study: None. This fly was described by Hesse (1967) as this work was being completed. I have reproduced Dr. Hesse's description and figures.

Immature stages: The larvae from which these flies were reared were found in loose soil in association with

the egg packets of the brown trek locust of South Africa (*Locustana pardalina*).

Ecology and behavior of adults: Unknown.

Distribution: Ethiopian: *Psiloderoideus mansfieldi* Hesse, 1967.

Genus *Cyrtomorpha* White

FIGURES 95, 222, 320, 581, 587, 875, 876, 877

Cyrtomorpha White, Papers Proc. Roy. Soc. Tasmania, p. 185, 1917 (1916). Type of genus: *Cyrtomorpha paganica* White, 1917, by original designation.

Strange, comparatively small, flies of more or less cyrtid-like appearance with rather convex mesonotum, especially in front of the scutellum and with extraordinarily broad, large, inflated abdomen, very much wider than the thorax, which bears minute, appressed, setate pile. The head is small, much more narrow than the thorax and appears to be attached low on the thorax largely because of the elevated mesonotum. The mesonotum is more convex than usually seen in bee flies, both anteriorly and posteriorly but a little more so behind in front of the scutellum. The antennae are minute; the proboscis is short and in some species reduced to a mere stub, not visible from the sides. Oral recess or buccal cavity on the bottom of the head. Male eyes not quite holoptic. The venation is peculiar. The wing is broad; the discal cell is wanting; there are 3 branches to the radius, hence only 2 submarginal cells, and the marginal cell is quite short and narrow. Second vein ends barely beyond the first vein. There are 3 branches to the medius and the anterior 2 branches anastomose a short distance from the radiomedial crossvein. The anal cell is narrowly open; while the wing is broad at the base, the alula is almost absent and is quite linear.

These flies are restricted to Tasmania and Western Australia.

Length: 4 to 5 mm.; wing, 4 mm.

Head, lateral aspect: The head in this aspect is not quite globular because the upper half of the head slopes backward from the middle of the face to the vertex and is less extensively produced than the lower half. The occiput is only moderately extensive but rather strongly convex from the middle outward to the eye margin. Its pile consists of short, stiff, appressed, bristly hairs, those at the bottom of the head more erect. The front is plane with the eye immediately in front of the antennae, gradually rising and swelling toward the vertex, which is rather conspicuously elevated above the eye margin, and there is a small raised ocellar tubercle in the center in females. In males the front is restricted to a small, sunken triangle above the antennae and the vertical triangle is likewise sunken beneath the eye margin and only the equilateral ocellar triangle is visible. The eye is quite large, occupying most of the head in both sexes, the posterior margin entire and in the male shows an overgrowth backward and downward on the upper half, encroaching on the occiput, which in consequence

is greatly reduced. Male with the eye almost touching the middle, separated by not more than the thickness of the antennal style, or apparently more widely separated in other species according to Roberts (1929).

Although Roberts describes the proboscis as short, not as long as the head and palpus very small, one-segmented, in the material before me the proboscis is a mere, minute stump, and I find no trace of the palpus. Antennae attached at the middle of the head and quite small. From the lateral aspect the extremely short first segment cannot be seen because of a slight overgrowth of the eye anteriorly on each side. The second segment is also very short and beadlike and both have a few apical setae above and below. The third segment has a somewhat bulblike swelling at the base, not wider than the second segment, beyond which it is rather strongly narrowed, the cylindrical half only about half as wide as the base. It bears a bristle-tipped style of the same thickness as the outer part of the third segment and as long as this segment.

Head, anterior aspect: The head is short-oval being distinctly wider than high, tending to be flattened both dorsally and ventrally and also a little on the sides, so that actually there is a slight subrectangular appearance to the head in the male and a more oval appearance in the female. In the female the eyes are separated by about twice the width of the ocellar tubercle. The frontal pile in the female is scanty, stiff, bristly, suberect, and not very long. The antennae are adjacent at the base. The face is extensive, somewhat convex, the oragenal recess confined to the bottom of the head, broad, nearly circular and since from a central view the eyes diverge posteriorly, the genal area is largely triangular on each side. The oral recess is rather deep with vertical sides behind. Pile of face and gena rather long, fine, more or less curled, curved downward, and of a shining brassy yellow. Tentorial fissure shallow.

Thorax: The thorax is short and compact and strongly humped on the mesonotum. The anterior and posterior part of the mesonotum is almost steep and is rounded. Head and especially abdomen decumbent. Prothorax very small and reduced in extent. The humerus is small, oval, and somewhat flattened with the posterior corner rounded. The mesonotum is yellowish to reddish brown laterally with the central part either black or with 3 wide, black vittae, either shining or partly dulled by pollen that consists of microscopically small rounded, flattened scales. Scutellum thick, convexly rounded posteriorly, comparatively short, its margin and disc and the mesonotum with comparatively dense, coarse, erect, rather bristly pile of no great length. Mesopleuron over nearly its whole surface with pile similar to the mesonotum. Pteropleuron, metapleuron, hypopleuron, and sternopleuron without pile, but with sparse, microscopic scales. Squama short with thickened apilose margin. The outer section of the squama is somewhat larger. Metasternum small, especially reduced behind the scutellum; its most extensive part consists of a narrow, rounded, oblique, lateral fold.

Legs: The legs are relatively short and stout. Middle and hind femora each only slightly longer than the anterior femur and each with a fringe of fine, erect or slightly appressed pile, nowhere longer than the width of the tibia. The femora are loosely covered with microscopic scales. All of the tibiae are similarly pilose but the pile is somewhat shorter than on the femora. The anterior tibia ventrally has a row of oblique, short, numerous, microscopic setae similar to that which extends onto the tarsi. All of the tarsi are quite short including the hind pair and covered with microscopic, appressed setae. Claws and pulvilli small, the former short and sharp, the latter wide, broadly rounded at the apex and as long as the claws.

Wings: The wings are quite broad and relatively short and hyaline, except that the whole surface is covered with coarse, brownish villi. The first vein ends only a little distance beyond the middle anterior wing border; the second vein ends also only a short distance beyond the end of the first vein a distance a little less than that which lies between the ends of the first vein and the auxiliary vein. There is only 1 submarginal cell, the third vein not branched. The radical sector is as long as the first section of the third vein, ending at the anterior crossvein. There is no discal cell and the medius branches or forks a short distance beyond the anterior crossvein equal to approximately the length of the anterior crossvein. There are 4 posterior cells all widely open, and the third vein ends barely before the apex of the wing. Anal cell open, axillary lobe large but alula wanting. The ambient vein is wanting, since the costa ends at the apex of the wing. All of the veins are quite stout, but the branches of the medius are somewhat reduced or even semiatrophied at the wing margin.

Abdomen: The abdomen is very wide, much wider than the mesonotum, especially in the female, and it is short and presents a rather short, rounded appearance from above; in shape and width it reminds one of *Usia* Latreille. There are 7 tergites visible from above with the abdomen tilted forward a little. If viewed directly from above only 5 are visible, the last 2 are a little shorter and strongly turned down due to the convexity of the abdomen. On each tergite there is a prominent, transverse, posteriorly arched, foveate depression on each side near the middle and resting on the the anterior border of the tergites and in addition what appears to be spiracular depression outside of these foveae, yet far from the lateral margin. Viewed from beneath, the brown sclerotized sternites are crowded together, each with a wide, extensive, lateral, yellow, apparently non-sclerotized area, and there is a similar broad, shining, yellow obtuse triangle at the base in the middle of the first tergite, the area much wider than the scutellum. Also, viewed from below, two additional tergites can be discerned in the female, each rounded and cuplike and recessed within each other and both of these recessed within the seventh tergite. Female genitalia sunken and without any spines. Male genitalia small; the 2 main

dististyli and basimeres lying side by side and recessed within the ninth tergite.

The male terminalia from dorsal aspect, epandrium removed, show a short, compact rather wide structure with the basistylus quite short and with very peculiar dististyli, wide, obtuse and shaped much as an agaric-type funguslike apex. There is a strong bridge across from the ramus. In the lateral aspect the dististyle is even more peculiar, the basal part large, triangular, produced ventrally downward and pointed, the apical part club-shaped, turned downward and pointed backward and connected by a very narrow neck. The epandrium has unusual depth and is quite short.

Material studied: A male and female of this genus taken in Western Australia.

Immature stages: The larvae of these flies are predators on the eggs of locust. See discussion under life histories.

Ecology and behavior of adults: I have seen no records of the behavior of these flies.

Distribution: Australian: *Cyrtomorpha flaviscutellaris* Roberts, 1929; *paganica* White, 1917.

Genus *Platypygus* Loew

FIGURE 331

Platypygus Loew, Stettiner Ent. Zeitung, vol. 5, p. 127, 1844.

Type of genus: *Platypygus chrysanthemi* Loew, 1844, by monotypy.

Popsia A. Costa, Atti Roy. Accad. Sci. Napoli, vol. 1, p. 51, 1863.

Type of genus: *Popsia ridibundus*, 1863, by monotypy.

Paramonov (1929), vol. 11, treatment of Palaearctic species.

Engel (1933), pp. 121-122, key to 8 Palaearctic species.

Quite small flies that are rather strongly humped upon the mesonotum. They are generally blackish with a considerable amount of yellow markings upon head, thorax, or abdomen, or all three. The head is subglobose with the eye large and rounded, but there is much variation in the extent of the occiput, which varies from very short indeed in species like *ridibundus* Costa or *pumilio* Loew, to very extensively produced backward in species like *melleus* Loew and *melinoproctus* Loew. Probably all of those forms with the extraordinarily lengthened occiput should be placed within the genus *Cyrtisopsis* Ségué, especially because of the variation of the length of the proboscis which is quite long in *Cyrtisopsis*, but short, not as long as the head in *Platypygus chrysanthemi* Loew, the type-species. Also, the very curiously lengthened occiput of *Ceratolaemus xanthogrammus* Hesse should be noted. Hesse (1938) made this fly a subgenus of *Platypygus* Loew, although the absence of the discal cell and appearance of the wing seem to ally it to *Cyrtosia* Loew. All of the species of *Cyrtosia* Loew appear to have a rounded head and short occiput except *nitidissima* Engel, where it is extensive behind.

Although the discal cell has shown a tendency to be wanting in the subfamily Mythicomyiinae, I am inclined to believe that its presence or absence is more significant than the highly variable postociput. Because in the fly *Ceratolaemus* Hesse the wing is much more like *Platypygus* Loew in its general form, I leave it as a genus related to *Platypygus*. Note that the third antennal segment has a large, tapered, bristly, setate microsegment ending in a spiny style; palpus and alula are absent. Species of *Platypygus* Loew are apt to have the apex of the abdomen compressed, high vertically, and truncate apically as shown in Engel (1933, Figure 58).

Platypygus Loew is found in Southern Europe, Asia Minor, and South Africa.

Length: 1.8 mm. (in *pumilio* Loew); usually 3.5 to 5.5 mm.

Head: A little narrower than the thorax and almost rounded when seen from above, but when viewed in profile it is much longer than high, owing to the considerable puffed-out occiput (which is even more conspicuously produced below than in the genus *Cyrtosia*), into a large triangular shieldlike projection, one on each side of the posterior mouth opening; frons a little broader above, nearer the vertex than below, where it is somewhat hollowed out above the base of the antennae, and when seen in profile its sides form a weakly convex line with the much shorter, porrect upper part of the face (below the base of antennae), which is then abruptly directed vertically down at an angle of 45 degrees forming the upper side margins of the mouth; eyes widely separated in both sexes and with the facets of equal size all over but always with a minute triangular indentation on the anterodorsal margin, a short distance above the base of the antennae; proboscis long (a little longer than the length of the head) or very long (about 3 times the length of the head); palpi minute, very short and often concealed in the opening of the mouth; antennae much resembling that of *Cyrtosia*, the two basal segments very short and equivalent in length and the third segment pyriform, with an apical style that is usually thickened by the presence of microscopic pubescence and always bearing a short apical sensory seta.

Thorax: The thorax is very deeply humpbacked with the pronotum and metanotum strongly developed; the attachment of the head to the thorax is exceedingly low, being immediately above the base of the elongate anterior coxa, so that the summit of the head is on an almost straight line with the notopleural suture.

Legs: The legs are neither strong nor elongate, usually pale except the apical tarsal segments obscured, and even blackish owing to the minute pubescence consisting of microscopic black bristles.

Wings: Wings with a venation much less reduced than in *Cyrtosia* as the 1st M cell is always present and the R sector forms 2 branches; the auxiliary vein does not fade away in the cell before reaching the costa. The costa latter is strong and thickened for a short distance

beyond the tip of the third vein; 1st anal cell always open; alula absent; anal lobe well developed; squama almost bare; halteres with a short stalk and a large knob.

Abdomen: The abdomen is distinctly broader than the thorax, but it may be as broad as, or narrower than, the thorax; it consists of 7 or 8 apparent segments and the apical, sternite is large and usually conceals the genitalia; in the male, however, the crossed branches of the forceps and in the female 2 short oval cerci project outward.

Material available for study: I have studied the series of these flies within the British Museum (Natural History), and my illustrations are taken from these flies, supplemented by figures taken from Engel (1933). I have supplemented the description I made in London with quotations from Efllatoun's excellent description of this genus (Efllatoun, 1945).

Immature stages: Unknown.

Ecology and behavior of adults: Efllatoun (1945) notes that *Platypygus (Cyrtisiopsis) melleus* Loew is common in the eastern desert of Egypt and is an excellent hoverer; he states that he has often seen it hovering over bushes and blooms of *Zygophyllum album*, almost always at the extreme edge of a Wafi; usually at extreme edge and in the shade of a boulder near the grotto housed webs of arachnids.

Distribution: Nearctic: *Platypygus americanus* Meander, 1950.

Palaeartic: *Platypygus algirus* Paramonov, 1929; *bellus* Loew, 1869; *chrysanthemi* Loew, 1844; *depressus* Loew, 1855; *kassanovskiji* Paramonov, 1929; *kurdorum* Paramonov, 1929; *kurdorum persicus* Paramonov, 1934; *lativentris* Loew, 1873; *limatus* Séguy, 1963; *maculiventris* Loew, 1874; *melinoproctus* Loew, 1873; *melleus* Loew, 1856; *punilio* Loew, 1873; *ridibundus* (A. Costa), 1863 (as *Popsia*) [= *tauricus* Paramonov, 1926]; *turkmenorum* Paramonov, 1929.

Ethiopian: *Platypygus natalensis* Hesse, 1967.

Genus *Cyrtisiopsis* Séguy

FIGURES 330, 600, 997, 998, 999

Cyrtisiopsis Séguy, Ann. Mus. Storia nat. Genova, vol. 55, p. 80, 1930d. Type of genus: *Cyrtisiopsis singularis* Séguy, 1930, by original designation.

Minute, shining, blackish flies with large, opaque, white halteres and sometimes with narrow, yellow postmargins to some of the abdominal segments. The head is quite elongate, and including the eye, longer than high. The occiput is very extensive both above and below but more so ventrally, so there is an extensive grooved gular region which, however, has no setae. The males are widely dichoptic, the proboscis is elongate but rather strongly thickened progressively toward the base. It is at least $1\frac{1}{2}$ times as long as the head length. The genofacial area is rather strongly compressed laterally,

because of the extensive anterior development of the eyes. The hyaline wings have black veins, 1 submarginal cell, 4 posterior cells. The anterior intercalary vein at the end of the discal cell is short. The anal cell is widely opened. The auxiliary vein is complete. The ambient vein ends at the apex of the wing.

These flies are known from Italian Somaliland and South Africa.

Length: About 2 mm.; wings about $1\frac{1}{2}$ mm.

Head, lateral aspect: The head is elongate, much longer than high; the occiput is extensive both above and below, more so below, where the long gular region has a medial fissurelike groove. From below, the eyes are obliquely or diagonally excavated. From the dorsal aspect the ocelli are set anteriorly ahead of the postero-dorsal corners of the eye, which are broadly rounded. The antennae are set closely adjacent near the anterior part of the head. There is a distinct, comparatively long, though narrow, facial area before the beginning of the plane, nearly vertically, laterally compressed oragenal cup. The gena proper appears to be absent, due to the encroachment of the eye, and consequently there is no tentorial fissure. The proboscis is large, at least $1\frac{1}{2}$ times as long as the length of the head, and it is progressively thickened and widened toward the base. The labellum is quite slender, almost filiform. Palpus filiform.

Head, anterior aspect: The frons has a distinct, extensive, scooplike or shallow depression extending to the base of the large, quite low ocellar tubercle. The ocelli are small, the posterior ocelli set far apart. Antennae adjacent at the base. At the vertex the eyes are separated by a little less than one-third the head width. The oral opening is quite narrow.

Thorax: The thorax is slightly wider than the head, the mesonotum a little longer than wide with a distinct convex appearance from the side. It is not excessively humpbacked. The surface is dully shining with microscopic, scarcely evident setae, which are more or less appressed. Pleuron shining black, edged with pale brownish yellow, on the propleuron, lateral margins of the mesonotum, posterior margins of the mesopleuron, and with a diagonal whitish spot on the postalar callosity. The shining humeri are brown. The halteres are quite large and opaque yellowish white, and quite conspicuous with a rounded, swollen knob.

Legs: Legs shining black throughout with very microscopic setaelike pile. The claws are very slender; the pulvilli are well developed. All the femora are slightly thickened especially through the middle and the hind femur is only slightly longer than the anterior middle femur.

Wings: Quite hyaline, relatively smooth with iridescent reflection, and brownish-black veins. The wing is elongate oval with rounded apex. There is only 1 submarginal cell but 4 posterior cells, with the upper anterior intercalary vein at the end of the discal cell rela-

tively short. The anterior crossvein enters the discal cell at the middle; the anal cell is widely open and while the axillary lobe is moderately wide, I cannot find an alula on my material.

Abdomen: The abdomen is relatively short, no wider than the thorax, tending to be more or less truncate at the apex of the sixth segment in males. The fifth and sixth tergites in the species before me, *crassirostris* Hesse, paratype, have very thin, narrow, yellow post-margins to these tergites. Other tergites are recessed. The male terminalia are black, rather large, terminal

and protrude from this truncated, large, circular terminal ending of the abdomen.

Material available for study: Two male paratypes of *Cyrtisiopsis crassirostris* Hesse furnished me through the generosity of Dr. Hesse.

Immature stages: Unknown.

Ecology and behavior of adults: Found on the heads of composite flowers in South Africa, the long proboscis used in feeding.

Distribution: Ethiopian: *Cyrtisiopsis crassirostris* Hesse, 1967; *singularis* Séguy, 1930.

Subfamily Mythicomysiinae Melander, 1902

Very small to minute flies, some of which are even less than a millimeter in length and in general smaller than the members of the related subfamily Platypyginae. Both subfamilies have a tendency to what Hesse (1967) calls a quadriarticulate antenna. All of them are humpbacked, but some genera more so. This is especially true of *Cyrtosia* Perris, and in the subfamily here discussed, it is particularly true of the species of *Mythicomysia* Coquillett. These flies may be almost entirely shining black as in *Glabellula* Bezzi, or they may have much yellow or pale coloration as in most *Cyrtosia* species, but more generally, *Mythicomysia* species are pollinose and grayish black, and pale color is usually much reduced.

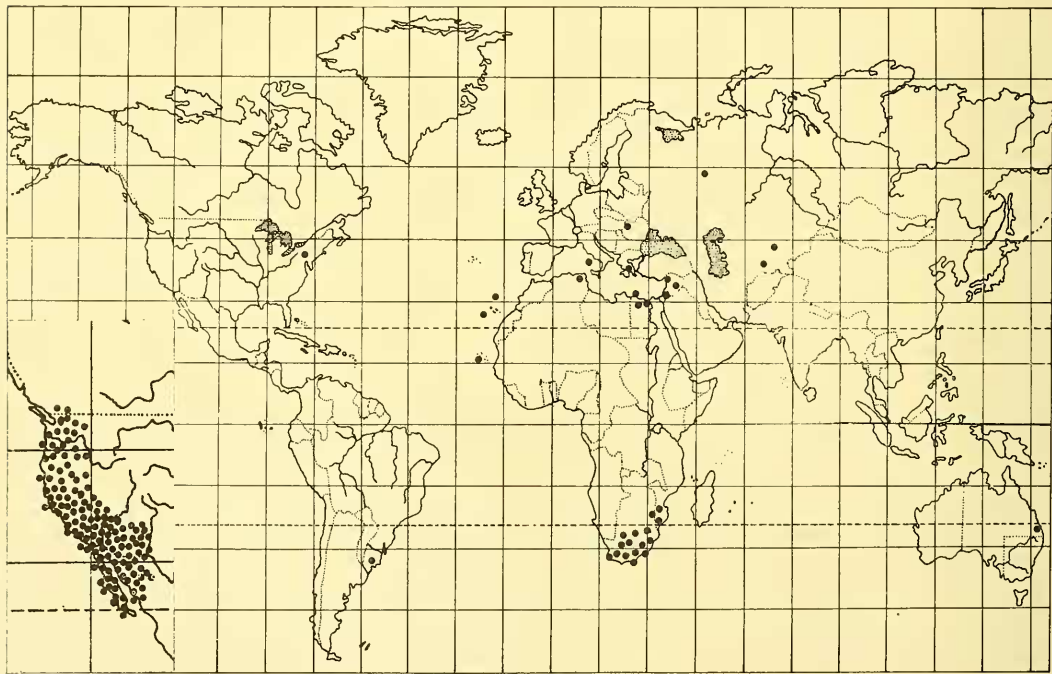
In this subfamily the radial sector never has more than 2 branches, the first of which, the second vein,

characteristically always ends in the first vein and does not independently reach the costa; or, the second vein may be vestigial, fused with the first vein, or completely absent.

The third vein is unbranched. In some genera the fourth and sixth veins are apt to be evanescent, faint, or absent. The first and second basal cells are apt to be joined by the loss of the vein dividing them. It should be noted that the discal cell is sometimes wanting as in *Doliopteryx* Hesse, and *Euanthobates* Hesse where it has been lost by fusion with the third posterior cell and lost in the same way in *Empidideicus* Becker, but in *Glabellula* Bezzi lost by fusion with the large second basal cell.

Hesse (1967) has discovered other new genera that clearly belong in this subfamily, such as *Pseudoglabell-*

MYTHICOMYIINAE



TEXT-FIGURE 39.—Pattern of the approximate world distribution of the species of the subfamily Mythicomysiinae.

lula. Two tribes may be recognized: the Empidideicini with second vein absent, and Mythicomyni in which it is present.

The subfamily Platypyginae is separated from the subfamily Mythicomyni by the presence of a distinct and complete second vein ending well beyond the end of the first vein, but it should be noted that the discal cell may be present or absent in both subfamilies. Evolutionally we here rank the medial field as more unstable than the radial field since in so many families of Diptera from simuliids to phorids, etc., this seems to be true. This subfamily, the Mythicomyni, appears to have a much wider distribution throughout the world than the Platypyginae. The genus *Mythicomymia* Coquillett has reached an extraordinary development in the southwestern United States. This genus is also known from a single species at Montevideo, Uruguay, collected there by F. Edwards. He notes that the males fly in small swarms in sunlight. The nearest relative of *Mythicomymia* Coquillett appears to be *Aethiophilus* Hesse from South Africa.

Mythicomymia Coquillett has been shifted back and forth from the Rhagionidae (Leptidae) to Empididae

to Bombyliidae. Eleven species had been described chiefly from the southwestern United States, another species from Uruguay; as a result of assiduous collecting Melander (1960) described 136 new species or varieties from the southwestern United States. The deep canyons emerging from mountains of these western states and particularly from California have resulted in a curious isolation and a species-forming situation, which Melander (1946) likens to Gulick's description of species formation of snails in Hawaiian valleys.

The genus *Mythicomymia* Coquillett is very peculiar. In this genus the basistylus, or as called by others the penis sheath, is absent. This genus is characterized by a large, triangular form in lateral aspect, with extensive, free, basal ejaculatory apodeme and a curious epandrium shaped much like a boomerang. From the dorsal aspect the base of the aedeagus is large and egg-shaped and there are winglike structures on the apical half, which we tentatively call accessory apodemes. There is an especially long, curious aedeagal apodeme lying on each side of the basal ejaculatory apodeme which is shaped like a long hockey stick.

KEY TO THE GENERA OF THE SUBFAMILY MYTHICOMYIINAE

1. The first vein ends near the middle of the wing. The second vein is complete but ends in the first vein, making a small, triangular cell 2
- The second vein is vestigial or absent 6
2. The discal cell is absent 3
- The discal cell is present 5
3. The second basal cell is much larger than the first due to fusion of the second basal cell with the discal cell; from the combined cell four veins are emitted setting out 4 posterior cells (Holarctic, Ethiopian) *Glabeulula* Bezzi
- The loss of the discal cell is due to its fusion with the third posterior cell 4
4. No second basal cell present. The anterior branch of the fourth vein atrophied or wanting completely on the basal half, anal vein faint or absent and the fifth vein tending to be atrophied basally (Ethiopian) *Doliopteryx* Hesse
- Second basal cell distinct and distinctly separated from both discal and first basal cells; consequently only 3 veins proceed from the second basal cell. The first posterior cell is much more narrow and narrowed apically and opens upon the costa above the wing apex; the fourth vein divides into two branches leaving a wide, triangular second posterior and apical cell. There is no projecting pronotal lobe (Ethiopian) *Pseudoglabeulula* Hesse
5. Vein between first and second basal cell evanescent. Axillary lobe narrow, the anal cell closed and the anal vein faint or evanescent. Whole wing about as wide near the apex as near the base (Ethiopian) *Aethiophilus* Hesse
- Vein separating the first and second basal cells strong and distinct. Anal cell open and anal vein distinct. The wing is broad basally, often quite broad, with a prominent, wide axillary lobe (Nearctic, Neotropical) *Mythicomymia* Coquillett
6. Discal cell present. Vein separating first and second basal cells quite faint or absent. Intercalary vein quite short (Ethiopian) *Anomaloptilus* Hesse

- Discal cell absent, confluent with third posterior cell . . . 7
7. Face very short and eye relatively small. Proboscis with basal part as long as the eye but distal part often extremely long, from 2 to 3 times as long as head. Wing with first posterior cell quite narrowed apically. Anal cell narrowly open or closed in the margin. Vein separating first and second basal cells distinct, well formed . . . 8
- Face jutting forward as a short, peaklike, triangular elevation. First posterior cell distinctly widened and flared apically. Anal cell widely open. Vein separating first and second basal cells faint or wanting 9
8. Ventral part of head with a "gular" groove, or sulcate; this groove bearing curious, downward projecting, fingerlike, coecalike or straplike processes, arranged much as in a comb on each side of the head (Ethiopian) *Euanthobates* Hesse
- Grooved lower portion of head completely without any trace of protruding, coecalike processes (Ethiopian) *Euanthobates* (*Acoecus*, new subgenus)
9. Style of third antennal segment virtually absent, style minute and visible only under high magnification. Head more elongate due to a more strongly developed occiput. Anterior branch of medius thrust forward, thinned, weak and evanescent distally (Egyptian) *Leylaiya* Efflatoun
- Style of third antennal segment prominent and well developed. Anterior branch of medius not evanescent, ending below apex of wing 10
10. The anterior ocellus lies in line with the posterior ocellus. Abdomen wider than the thorax and flattened (Palaeartic) *Empidideicus* (*Cyrtoides*) Engel
- The anterior ocellus lies in front of the others, forming a triangle. Abdomen not wider than thorax (Holarctic, Ethiopian) *Empidideicus* Becker

Genus *Mythicomyia* Coquillett

FIGURES 101, 102, 342, 347, 596, 605, 884, 885, 886

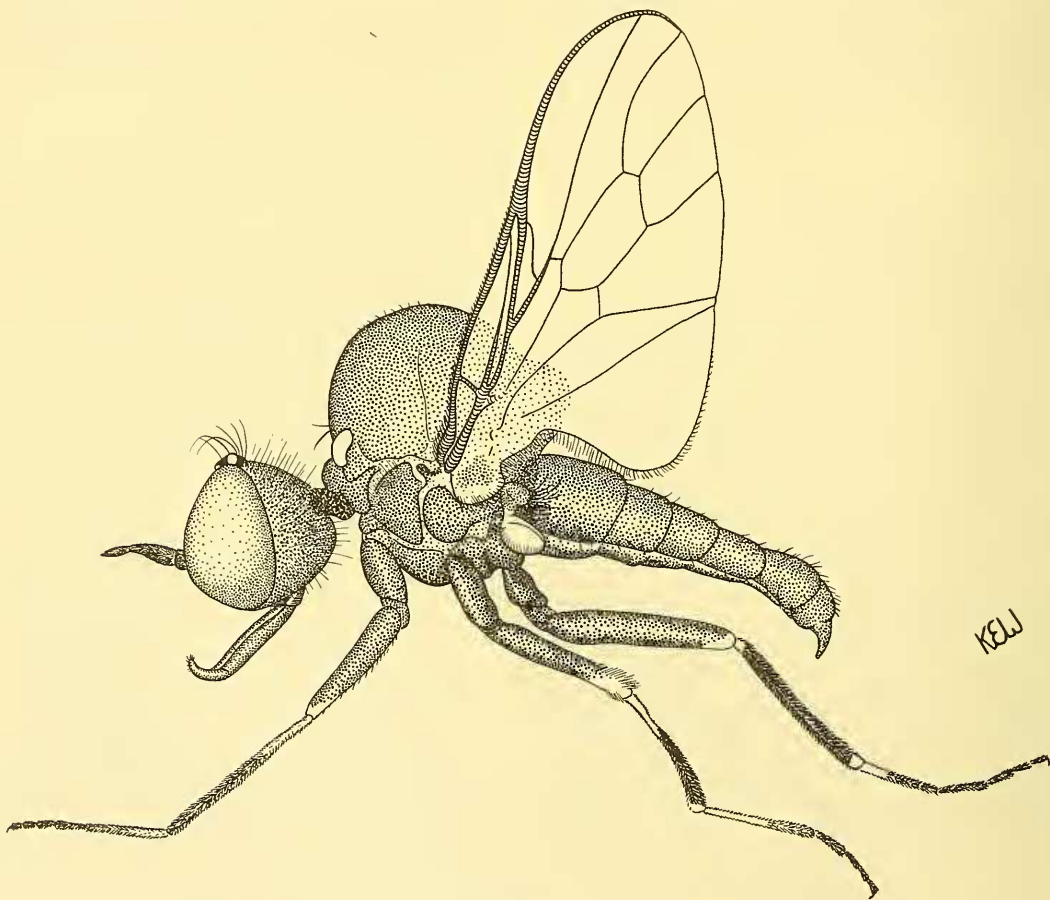
Mythicomyia Coquillett, Ent. News, vol. 4, p. 209, 1893. Type of genus: *Mythicomyia rileyi* Coquillett, 1893, monotypy.

Melander (1902), pp. 337-338, treats *Mythicomyia* as an empidid. Melander (1961), pp. 163-179, key to 136 species and subspecies.

Very minute flies, seldom more than two millimeters in length and often much less. Males are very strongly humpbacked and darker in color, hence sexes are not easily associated. They are distinguished from *Glabellula* Bezzi by the presence of a complete discal cell and by the strongly holoptic eyes of the male. In addition, the abdomen is much more slender, somewhat lengthened and attenuate compared to the short, stout, robust, plump abdomen of *Glabellula* Bezzi. The antennae are

longer, more slender and attenuate upon the style of the third segment. The wing is strongly widened basally so that the axillary lobe is triangular with a rounded angle. Anal cell narrowly open, sometimes closed in the margin. In both genera the second vein is very short but well formed, ending in the first vein much like a cross-vein resulting in a short, triangular marginal cell.

This genus has had a checkered history. Its author, Coquillett (1893), founded it upon a single specimen, he named *rileyi*, and placed it within the Empididae. Melander (1902) in his review of the Empididae kept it within this family and made it the basis of the subfamily Mythicomyiinae, for flies with abbreviated second vein. Greene (1924) was the first to review the various changed allocation of the genus, noting that Williston, Osten Sacken, and Schiner located the genus within the Rhagionidae (Leptidae of authors). Both



TEXT-FIGURE 40.—Habitus, *Mythicomyia monacha* Melander.

Coquillett and Cresson (1915) placed these flies within the Empididae. Aldrich and Kertész in their catalogs located it within the Rhagionidae (Leptidae of authors).

It remained for Greene (1924) to assign it to its present position on the basis of the pupal characters of a fly of the unquestionably closely related *Glabellula* Bezzi, which was reared from a pupa taken from frass of an oak in the District of Columbia. I believe that Greene was correct in his assumptions. Later authors have accepted its assignment to the Bombyliidae on the basis of Greene's study.

The genus *Mythicomyia* Coquillett prior to 1960 was known from 12 species, 2 from Chile and Uruguay respectively, and the other 10 from the southwestern United States and ranging as far east as New Mexico. In 1960 Melander described 127 new species and 9 varieties, of which 92 were from southern California alone (including a few from the bays of Lower California) and 35 other species from southern California and additional western states, usually Arizona or New Mexico. Several species extended northward to Oregon or Washington, a few into Sonora. Two species, *rileyi* Coquillett and *armata* Cresson, are quite widespread in the western United States. The months they fly range from March to September but more commonly in April, May, or June, and again in September. Four species were collected in Arizona only, and 4 in New Mexico alone. Twenty more species were found in both California and Arizona. Nine other species were collected in both California and New Mexico for a total of 13, where I have collected some myself. One species is recorded from Montana, 3 or 4 from Utah, Nevada, Oregon, and Washington.

Length: 0.9 mm. to 3.5 mm., with very few species greater than 2.0 mm. in length.

Head, lateral aspect: The head is subglobular. The occipital component is conspicuous and extensive both above and below, both in males and females but especially in the latter. In lateral aspect the face and oragenal cup are produced beyond the eye. The face in length is about as long as the first two antennal segments and slopes forward and downward. The large oragenal cup is equally produced above and below. The eye is nearly circular, except the portion between the ocelli and the antennae, which is nearly straight, and the portion from the lower front to the face is nearly straight. The facets are minute and all alike. The posterior margin of the eye is entire. The occiput has a few, fine, erect, stiff, short, scattered hairs. The lower portion of the sublateral occiput has considerable loose, long pile. The occiput is at most only slightly concave where it is attached to the thorax. The front is pollinose. The face and oragenal cup are pollinose also and the face and front have a very few fine, scattered hairs.

The proboscis is moderately elongate and about as long as the head. It is slender with long, slender labellum. The palpus is composed of one curious, short, rather flattened, laterally convex, oval segment, which is barely longer than wide and bears a long, slender

bristle at the apex; there are 1 or 2 other basal bristles on the outer margin. The palpus appears to be more or less hollow on the median surface. The antenna is somewhat elongate and relatively slender, but considerably shorter than the head. The first segment is very short, scarcely more than half as long as the second; the second segment is about as long as wide; and the third segment is widest just beyond the base where it is a little wider than the second segment. This third segment is somewhat narrowed apically, rather flattened and bears a conspicuous, flattened, rather long microsegment which appears to have a minute, short additional microsegment at its apex. The antenna is everywhere micropubescent. The antenna is attached at the middle of the head.

Head, anterior aspect: The head is about the same width as the thorax or in some species narrower. The face is separated from the front by a transverse groove or furrow in females. The eye in the male is holoptic touching in the middle for a distance of one-third of the total length of front and vertex. The antennae are adjacent and touching. The small front is triangular, pollinose in males and smaller than the triangular ocellar tubercle, which is only moderately raised above the eyes. The ocelli are large, especially the anterior ocellus, and all three rest at the margin of the eye in the male. The female front has parallel sides; its width is a little more than one-fourth the width of the head. The oral opening is triangular, though a little rounded anteriorly and is unusually deep. The medial roof has 3 or 4 rather long, slender, erect hairs on each side. The inner edge or wall of the oragenal cup is quite sharp. I can find no trace of gena or tentorial fissure.

Thorax: The thorax is high with a strongly humped and convex mesonotum, which is relatively short in length. The mesonotum is rather dull, more or less opaque, pollinose, with several rows of very minute, microscopically erect setae. The thorax is generally black or dark brown in color and the humerus, notopleuron and scutellum, and upper mesopleuron are apt to be pale yellow in color. Sometimes only the humerus and postalar callosity are yellow. The hypopleuron may be black or yellow. The upper mesopleuron may have a few long, stiff hairs; the remainder of the pleuron is micropubescent only; scutellum comparatively thin and flattened with several long, erect, stiff hairs on the disc. The squamae are short with a few scattered, stiff hairs; halteres with a short stalk and a very large, thick, slightly elongate club at apex as long as the stalk and divided dorsally by a curved, fissurelike crease.

Legs: The legs are short, often partly yellow, partly black. The femora are a little thickened, the anterior tibiae have several rows of minute, subappressed setae and the tibia is distinctly longer than the femur; posterior femur sometimes a little arched or bent with quite microscopic pubescence and a few scattered, suberect setae. The posterior tibia likewise has some scattered setae. The pulvilli are short, rounded, wide; claws minute and slender, strongly curved at the apex.

Wings: The wings are broad both at apex and base, the base not wider than the middle of the wing. The third vein has 2 branches, the anterior branch is quite short and ends in the first vein. There are 4 posterior cells all very widely open. The anterior crossvein enters the large, relatively long, discal cell at the basal sixth, therefore first and second basal cells are of nearly equal length. The auxiliary vein appears to be reduced and ends in the first vein or simultaneously with it in the costa. The intercalary vein is about half as long as the medial crossvein, the anal cell is open, the axillary lobe large, the alula wanting or reduced to a mere linear band. The ambient vein is absent but the posterior margin of the wing has a fringe of fine hairs and the entire surface of the wing is densely covered with minute, short, microscopic scales or quite flattened scale-form hairs, which are iridescent.

Abdomen: The abdomen is depressed or decumbent, obtuse, and rather plump and is largely black with yellow posterior margins in some species. The pile is setae or bristly consisting of several loose, scattered rows more or less flat-appressed on each tergite, and the last row extends well over and beyond the posterior margin. It is somewhat more dense laterally but equally stiff and bristly. I find 7 segments in the male and female. The male hypopygium is a broadly oval, rather flattened plate with laterally recurved sides containing the slender, elongate genitalia directed forward below.

The male terminalia from dorsal aspect, epandrium removed, show a very peculiar form in which the basistylus or so-called penis sheath is absent, and all of the remaining structures except two apodemes are concentrated forward on the outer apical half. The basal part of the aedeagus is quite large and bulb-shaped or egg-shaped. The epiphallus with enclosed aedeagus and ejaculatory duct, is small, short, and conical. I find no structure equivalent to the dististyli, although there is a very wide lateral structure apically, longer than wide, and extending directly outward and attached to a ramuslike bridge above the epiphallus which is possibly equivalent to the aedeagus. The basal ejaculatory apodeme is very, very long and there appear to be at least accessory apodemes in addition to a prominent, flared, leaflike lateral apodeme. The first of these accessory apodemes lies just across and opposite the base of the aedeagus. It forms an apically widened and rounded, leaflike structure. Arising from the ramuslike bridge across the epiphallus there is an extraordinarily long, backward process, very slender, extending directly by the side of the medial basal ejaculatory apodeme, or basal keel as it is sometimes called. It widens apically and is shaped like a hockey stick. From the lateral aspect the hypopygium is a curious, triangular affair with an odd, very tall or high, dorsally narrowing epandrium, very short in length and ventrally near the middle of the structure, extending obliquely downward and forward as a curious lobe. The cerci are equally peculiar in that they form a very tall, anteriorly convex

structure bulging forward and attached anteriorly to all of the epandrium except the downward lobe.

Material available for study: The late Dr. A. L. Melander presented me with several species and I have received several other species through the courtesy of Dr. Wirth and Dr. Karl Krombein of the National Museum of Natural History. Dr. Oldroyd presented me with a paratype of *Mythicomomyia pusillima* Edwards, a South American species. I have collected a few species in New Mexico both in 1959 and 1967 while on bee fly research expeditions. In 1959 I swept them from tall masses of goldenrod, *Solidago* sp., flowers in the Ruidoso Mountains. In 1967 they were swept from masses of flowers in White Mt., National Monument, New Mexico.

Immature stages: Unknown; however, Jack Hall, enthusiastic student of bee flies, recently recorded the rearing of this genus, on a multiple basis, from a bee cell.

Ecology and behavior of adults: The flies visit many flowering plants but are partial to some families and genera.

Melander (1960) in his final work on these flies, which he had so assiduously collected for many years, records collecting them upon 49 species of plants distributed among 33 genera of plants found within 19 plant families. They were more commonly found upon various species of *Eriogonum* such as *fasciculatum*, *inflatum*, *trichopodium*, *pusillum*, *gracile*, *thomasi*, *polifolium*, *nudum*, *kennedyi* *parishii*, and *subscaposum*, within the family Polygonaceae. The additional families frequented more sparingly consisted of Euphorbiaceae, Salicaceae, Boraginaceae, Rhannaceae, Caprifoliaceae, Polemoniaceae, Amaranthaceae, Loasaceae, Apocynaceae, Leguminosae, Zygophyllaceae, Labiatae, Capparidaceae, Rosaceae, Papaveraceae, Liliaceae, Bignoniaceae, and from the genera *Conyza*, *Baccharis*, *Chrysothamnus*, *Gutierrezia*, *Pectis*, *Eriophyllum*, *Isocoma* and *Tetradymia*, all within the family Compositae.

Melander notes that 54 species of *Mythicomomyia* were taken from one or more of 11 species of *Eriogonum* and the same species or some of them were also taken occasionally in other plants as well. The full list of plants upon which he collected the flies of this genus is given below.

Including the species already named, Melander collected flies of the genus *Mythicomomyia* Coquillett upon the following flowers:

Euphorbia polycarpus and *albomarginata*; *Croton californicus*; *Salix exigua*; *Adenostomum sparsifolium* and *fasciculatum*; *Conyza coulteri*; *Cryptantha intermedia*; *Baccharis pilularis*; *Chrysothamnus nauseosus*; *Ceanothus cordulatus* and *integerrimus*; *Sambucus glaucus*; *Rhamnus californicum*; *Lepidospartum squamatum*; *Hugelia virgata*; *Baeria aristata*; *Gutierrezia lucida*; *Tidestromia* sp.; *Pectis papposa*; *Apocynum androsaemifolium*; *Prosopis* sp.; *Petalonia thurberi*; *Eriophyllum confertiflorum*; *Larrea divaricata*;

Salvia vaseyi; *Wislizenia refracta*; *Isocoma acradenia*; *Fallugia paradoxa*; *Dalea californica*, *emeryi*, *spinosa*, *saundersi*; *Dendromecon rigida*; *Nolina parryi*; *Heliotropium curassavicum*; *Chilopsis linearis*; *Tetradymia canescens*.

Distribution: Nearctic: *Mythicomyia acuta* Melander, 1961; *agilis* Melander, 1961; *angusta* Melander, 1961; *annulata* Melander, 1961; *anomala* Melander, 1961; *antecessor* Melander, 1961; *apricata* Melander, 1961; *armata* Cresson, 1915; *armipes* Cresson, 1915; *atra* Cresson, 1915; *atrata* Melander, 1961; *aureola* Melander, 1961 [= *flavida* Melander, 1961]; *aurifera* Melander, 1961; *bibosa* Melander, 1961; *bilychnis* Melander, 1961; *bivulneris* Melander, 1961; *bucinator* Melander, 1961; *calva* Melander, 1961 [= *bella* Melander, 1961]; *californica* Greene, 1924; *caligula* Melander, 1961; *callima* Melander, 1961; *calva* Melander, 1961; *carptura* Melander, 1961; *collina* Melander, 1961 [= *actives* Melander, 1961]; *comma* Melander, 1961; *comparata* Melander, 1961; *compta* Melander, 1961; *concinna* Melander, 1961; *conrescens* Melander, 1961; *cressoni* Melander, 1961 [= *rileyi*, authors, not Coquillett]; *cristata* Melander, 1961; *crocina* Melander, 1961 [= *aspilota* Melander, 1961]; *cylia* Melander, 1961; *diadela* Melander, 1961; *dipura* Melander, 1961; *diopeda* Melander, 1961; *enoria* Melander, 1961; *eremica* Melander, 1961; *fasciolata* Melander, 1961; *flavipes* Cresson, 1915; *flaviventris* Melander, 1961; *formosa* Melander, 1961; *frontalia* Melander, 1961; *fulgida* Melander, 1961; *galbea* Melander, 1961; *gausa* Melander, 1961; *gibba* Melander, 1961; *gibbera* Melander, 1961; *gracilis* Melander, 1961; *habra* Melander, 1961; *hamata* Melander, 1961; *hiata* Melander, 1961; *hoplites* Melander, 1961; *hormatha* Melander, 1961; *hybos* Melander, 1961; *illustris* Melander, 1961; *imbellis* Melander, 1961; *indicata* Melander, 1961; *insignis* Melander, 1961; *intermedia* Melander, 1961; *introrsa* Melander, 1961; *irrupta* Melander, 1961; *lati-clavia* Melander, 1961; *lenticularis* Melander, 1961; *levigata* Melander, 1961; *liticen* Melander, 1961; *longimana* Melander, 1961; *marginata* Melander, 1961; *minima* Melander, 1961 [= *lucens* Melander, 1961]; *ministra* Melander, 1961; *minor* Melander, 1961; *minutula* Melander, 1961; *minuta* Greene, 1924; *mira* Melander, 1961; *mirifica* Melander, 1961; *mitrata* Melander, 1961; *modesta* Melander, 1961; *mulsea* Melander, 1961; *murina* Melander, 1961; *mutabilis* Melander, 1961; *napaea* Melander, 1961; *nigricans* Melander, 1961; *nitida* Melander, 1961; *nitidula* Melander, 1961; *occreata* Melander, 1961; *oporina* Melander, 1961; *optata* Melander, 1961 [= *diloga* Melander, 1961]; *orchestes* Melander, 1961; *ornata* Melander, 1961; *ornatula* Melander, 1961; *pruinosa* Melander, 1961; *pulla* Melander, 1961; *penicula* Melander, 1961; *petena* Melander, 1961; *petes* Melander, 1961; *petiolata* Melander, 1961; *phacodes* Melander, 1961; *phalerata* Melander, 1961; *pharetra* Melander, 1961; *picta* Melander, 1961; *pictipes* Coquillett, 1902; *platycheira* Melander, 1961; *polygena* Melander, 1961; *potrix* Melander, 1961; *pravipes* Melander, 1961; *pruinosa* Melander, 1961; *pulla* Melander

1961; *pusilla* Melander, 1961; *raeba* Melander, 1961; *rileyi* Coquillett, 1893; *robiginosa* Melander, 1961; *salpinx* Melander, 1961; *scapulata* Melander, 1961; *scutellata* Coquillett, 1902; *sorbens* Melander, 1961; *sugens* Melander, 1961; *tagax* Melander, 1961; *tenthos* Melander, 1961; *tibialis* Coquillett, 1895; *trifaria* Melander, 1961; *triformis* Melander, 1961 [= *chitona* Melander, 1961, = *monacha* Melander, 1961]; *tristis* Melander, 1961; *tubicen* Melander, 1961; *tumescens* Melander, 1961; *uncata* Melander, 1961; *vestis* Melander, 1961; *vilis* Melander, 1961; *virgata* Melander, 1961; *virgo* Melander, 1961; *vulnerata* Melander, 1961; *ostentata* Melander, 1961; *parma* Melander, 1961.

Neotropical: *Mythicomyia pusillima* Edwards, 1930.

Genus *Glabbellula* Bezzi

FIGURES 85A, 351, 597, 606

Platygaster Zetterstedt, Insecta Lapponica, Dipt., p. 574, 1838.

Type of genus: *Platygaster arctica* Zetterstedt, 1838, by monotypy. Preoccupied by Latreille, Hymenoptera, 1809; Schilling, Hemiptera, 1829.

Sphaerogaster Zetterstedt, Diptera scandinavica, vol. 1, pp. 22, 232, 30, 1842. Change of name. Preoccupied Dejean, Coleoptera, 1821.

Glabbella Loew, Beschreibungen europäischer Dipteren, vol. 3, p. 210, 1873. Type of genus: *Glabbella femorata* Loew, 1873, by monotypy. Preoccupied Swainson, Mollusc, 1840.

Glabbellula Bezzi, Zeitschr. syst. Hymen. Dipt. Teschendorf, vol. 2, p. 191, 1902. Change of name.

Pachyneres Greene, Proc. Ent. Soc. Washington, vol. 26, p. 62, 1924. Type of genus: *Pachyneres crassicornis* Greene, 1924, by monotypy.

Engel (1933), pp. 116-120, treats 5 species.

Melander (1950), pp. 142-143, key to 6 Nearctic species.

Minute, humpbacked, robust little flies, with short, stout, legs and with broad wing showing much reduction of venation. The auxiliary vein is evanescent or reduced, the first vein ends in the costa at the middle of the wing and the second vein, while stout, ends quickly in the first vein and in consequence forms a small, triangular cell; the third vein is unbranched. This genus is related to *Mythicomyia* Coquillett but has the discal cell confluent with the second basal cell, the males are dichoptic and it is much less strongly humped. Moreover, the fifth vein arises from the anal cell without the angulation that is normally found at the base of the discal cell. Engel (1933) notes that these flies look somewhat like small simuliids.

Glabbellula Bezzi is a rather small group of flies of widespread occurrence but rather rare in collections; see comments on ecology below. Melander (1950) described 5 additional species, 4 from California, making 6 species from the western United States; he notes that the American species have black legs, whereas those in the Old World have the tibial bases and tarsi brown. The flies are shining black, with often yellow markings over part of the fly. According to Melander (1950) they are also known from Canada, District of Columbia, Lapland, Siberia, Asia Minor, Syria, Turkestan, Palestine and the Philippines. In an earlier paper (1946)

Melander states that they have been taken in India and Australia, but I have not been able to find published references so stating.

Length: 1.0 mm. to 2.0 mm. All of the California species were very small, none over 1.25 mm.

Head, lateral aspect: The head is subglobular but curiously elongate, and the occipital portion is unusually well developed and prominent above and still more so below. The face is not very extensive but is quite high and becomes a little more extended at its lowest point, which is midway between the antennae and the bottom of the genae. Also, the antennae are attached midway between the ocelli and the lowest point of the face and the proboscis arises in the anteroventral corner of the head. The distance from the proboscis to the posteroventral corner of the occiput is as great or a little greater than the distance from the anterior base of the proboscis to the base of the antennae.

The pile of the occiput is restricted to a few, very minute, extraordinarily short, scalelike, submicroscopic setae along the middle and a few sharp, longer, slender setae behind the ocelli and a few fine, short, erect, stiff hairs along the ventral margin of the occiput, some beneath the eye and some placed more posteriorly. The eye is large, filling almost the entire lateral aspect, except the extensive occiput; its posterior margin is entire but broadly rounded. The facets are of uniform size throughout, each with a small central, circular yellow spot. The proboscis is stout and large and may be thrust straight downward or forward. Its length is equal the height of the eye; and the labellum is long but slender.

I can only find the palpus on the specimen where the proboscis is fully extended. What may be the palpus is a very slender linear structure lying immediately against the ventral edge of the gena and the base of the proboscis. I have been able to examine both sides of 2 well-preserved specimens without finding any further indication of the palpus.

Front in female flattened, pollinose, with 1 or 2 minute, erect setae. The antennae are attached at the upper third of the head and are relatively large though short, the first segment is a mere linear ring tucked against the upper edge of a ledge or shelf forming the lower limit of a distinct recessed, frontal depression. The antennae are adjacent. The second segment is 3 times as long as the brief annulus of the first segment, much wider both at base and apex and is broadly and tightly jointed to the large, oval, thick, anteromedially flattened or obliquely truncate third segment. Subdorsally the third segment bears a thick microsegment some $2\frac{1}{2}$ times as long as wide. Both the third segment and the microsegment are densely, coarsely, scaliform microsetate and there is some indication that the microsegment may be composed of 2 parts. Second segment also apically with some microsetae. All of these observations were taken at magnifications $90\times$ under several strong lights.

Head, anterior aspect: The head is very slightly wider than the thorax, although this may be due to some unnatural compression of the thorax in pinning. The eye is notched medially opposite the base of the antenna, and the upper part of the face has a depression beneath the frontal ledge which in section would be somewhat V-shaped. In males the eyes are dichoptic.

The front above the antennae is a pale yellow, shallow, shallowly excavated, hemicircular depression, bare, except that in the middle there is a large, central brownish spot bearing minute, erect fuzzlike pubescence. Above this excavated portion the vertex proper is shining brownish black with a few very scattered setae on each side. It is very slightly raised above the eye margin. The posterior ocelli are very far apart, the anterior ocellus only a little in front so that the ocellar triangle is very obtuse. The so-called ocellar tubercle is scarcely raised above the adjoining vertex. The posterior occiput is produced quite far behind the ocelli, broadly rounded and sloping inward with almost no trace of depression on either side, and with no tubercles and flanges below.

The oral opening is long and high, twice as wide below as above, with quite sharp medial edge and also the recess is deep. Anteriorly the oral recess has some strong, rather long setae which are somewhat flattened and scalelike. I am unable to determine whether this outer wall from the edge of the oral opening to the eye margin corresponds to gena or oraginal cup, as used elsewhere in this text, for there is not the slightest division of this part of the lower head nor any indication of a tentorial fissure.

Thorax: The mesonotum is rather high and strongly and equally arched both anteriorly and posteriorly, shining brownish black in color; the vestiture consists of rather moderately abundant, short, stiff, suberect setae pointed backward on the anterior half, pointed upward or forward on the posterior half. There are a few longer setae along the transverse suture and 2 distinctly stiffer, slightly longer setae in the posterior corner of the notopleuron. Scutellum thick, short, convex with similar setae to the mesonotum. The pleuron is likewise high and compacted, especially below, the coxae crowded together. It is likewise shining, brownish black with a little yellow on the humerus, the upper and anterior margin of the mesopleuron, laterally upon the very short propleuron, and again on the upper hypopleuron. The only pile upon the pleuron consists of a patch of quite flat-appressed, scaliform microsetae on the lower mesopleuron, the anterior pteropleuron and a small dense patch at the very top on the metapleuron beneath the haltere. Also, there are a few scattered setae on the metapleuron above the hind coxae. Upper mesopleuron with a few fine, short, erect hairs. Squama short with a fringe of short pubescence. Haltere with large, conspicuous elongate oval, closed knob.

Legs: The legs are unusually short, the femora quite stout, all the femora about equally swollen above and below. Both femora and tibiae with numerous, flat-

appressed setae and no outstanding spines or bristles. Dorsally on the hind tibia there is a row of very short, fine, erect or suberect short hairs and the apex bears a short, spinous bristle medially. The pulvilli are short and rounded, the claws slender and gradually curved.

Wings: The wings are broad, relatively short, wider basally and almost equally wide apically. The auxiliary vein is vestigial, the first, second, and third veins much stouter and blacker. The first vein ends near or just beyond the middle of the wing, the second vein ends in the first vein about midway from its origin of the costa and the third vein ends a short distance back from the end of the wing and joins the costa near the end of the costa. Ambient vein completely wanting, whole wing villose, the remaining veins colorless. The anterior crossvein lies opposite the end of the first vein. There are 4 posterior cells, the anal vein appears to be vestigial and represented by a fold, in which case the anal cell is open. The discal cell is wanting and there are 3 branches to the medius. Alula absent. Posterior margin of the wing with a fringe of relatively long hairs.

Abdomen: The abdomen is short, broad, rather thick, decumbent, thick and convexly rounded laterally, flattened through the middle, short oval viewed from above and covered with scanty, scattered, appressed, fine setae hairs, which extend beyond the posterior margins of the tergites. I find 8 segments in the female. The sternal area is rather narrow and the last sternite shows 2 long, platelike and pronglike lobes that overlap the apex of the abdomen below and overlap each other apically, leaving a recess within.

Material available for study: Before me are 2 paratypes of *Glabellula crassicornis* Greene (described as *Pachyneres crassicornis*). Also, I have seen Melander's species and the species *nobilis* Kertész, var. *palaestinis* Engel from material in the British Museum (Natural History).

Immature stages: Largely unknown; Greene (1924) figures the lateral aspect of one pupa of *crassicornis* Greene that was found in the frass from a decaying tree of *Quercus velutina* Lamarek in the District of Columbia; found April 15, the adult emerged April 20.

Ecology and behavior of adults: Melander (1950), who in 50 years collected only 19 individuals, 5 were new species, states that the adults frequent flowers. They have been taken upon flowers of mesquite, on *Rhamnus californica*, and in Manitoba upon strawberry blossoms. Four of the six American species are from California. Engel (1933) found them in flowers of *Polygonum* sp.

Distribution: Nearctic: *Glabellula crassicornis* (Greene), 1924 (as *Pachyneres*); *fasciata* Melander, 1950; *metatarsalis* Melander, 1950; *nanella* Melander, 1950; *pumila* Melander, 1950; *rotundipennis* Melander, 1950; *australis* Malloch.

Palaearctic: *Glabellula arctica* Zetterstedt, 1838; *canariensis* Frey, 1936; *femorata* Loew, 1873; *meridionalis* François, 1955; *nobilis* Kertész, 1912, *nobilis palaestinis* Engel, 1933; *unicolor* Strobl, 1910.

Ethiopian: *Glabellula mellea* Bezzi, 1908; *natalensis* Hesse, 1967.

Genus *Aetheoptilus* Hesse

FIGURE 344

Aetheoptilus Hesse, Ann. South African Mus., Part 6, vol. 50, p. 112, 1967. Type of genus: *Empidideicus* (*Aetheoptilus*) *zuluensis*, Hesse, 1967.

Very minute flies that are clearly related to *Empidideicus* Becker and regarded by Hesse as a subgenus of those flies. This fly is readily separated from *Empidideicus* Becker by the presence of the complete discal cell. Because of the closed anal cell, the shape of the veins at the end of the fused basal cells, I place it in a genus near *Mythicomyia* Coquillett; it appears to me to be the closest of all the South African *Mythicomyiinae* to the genus *Mythicomyia* Coquillett itself.

Flies that were collected Ndumu Reserve, Ingwavuma District, Zululand.

Length: 1.2 mm.; of wing 1.72 mm.

While Dr. Hesse indicated a subgeneric status for his new bee fly *Aetheoptilus* Hesse, 1967, I believe from my study of this subfamily that it deserves equal rank with related forms. His description is quoted below:

The deviation from the normal wing-venation of *Empidideicus*, as described by Becker (1907) and Engel (1933) and as is present in the South African species *Empidideicus turneri* Hesse, has gone a step further in a single female specimen from Zululand in which, in addition to the presence of a discoidal cell as in the subgen. *Anomaloptilus* Hesse there is also present a reduced or vestigial marginal cell as in species of *Glabellula* Bezzi, *Dolichopteryx* Hesse and the new genus *Pseudoglabellula*.

To accommodate it a new subgenus *Aetheoptilus* of *Empidideicus* is proposed provisionally, pending the discovery of more material of both sexes.

This new subgenus, as typified by this single female specimen, agrees with *Empidideicus* in most of its generic characters, but differs, apart from the presence of a distinct discoidal cell and a narrowish reduced marginal cell, in having the anal cell angularly acute apically and very shortly stalked, and in its broader frons, face and groove in head below.

From the subgenus *Anomaloptilus*, which also has a discoidal cell, it differs in the presence of a vestigial marginal cell, the apically acute and very shortly stalked anal cell, the more S-curved anterior vein of second posterior cell, more parallelogram-shaped third posterior cell, and in the cephalic characters mentioned above. As far as the wing-venation is concerned this subgenus appears to be even more primitive than *Anomaloptilus*. If the type of wing-venation of *Empidideicus* be considered as a specialization on an ancestral type in which reduction has taken place, a step nearer this ancestral condition is represented by *Anomaloptilus* where a discoidal cell still persists. On this assumption *Aetheoptilus* represents an even more primitive condition in which not only the discoidal cell is still found, but in addition there is also a vestige of the normal marginal cell of the ancestral type.

Material available for study: None. This fly was described by Dr. Hesse (1967) while this work was reaching final stages. *Aetheoptilus zuluensis* was described from a single female.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Aethioptilus zuluensis* Hesse, 1967 (as *Empidideicus*).

Genus *Dolipteryx* Hesse

FIGURE 323

Dolipteryx Hesse, Ann. South African Mus., pt. 3, vol. 35, p. 936, 1956. Type of genus: *Dolipteryx crocea* Hesse, 1956, by original designation.

Minute, humpbacked flies that are unique in possessing the greatest reduction in venation among the Bombyliidae. The antennae are similar to *Empidideicus* Becker, except that the style or microsegment is rather conspicuously pilose or bristly. The wing is broad and has only a single basal cell above which is a small triangular cell just as in *Glbellula* Bezzi, which I consider to be its nearest relative among known genera, and this small closed cell may be regarded as the marginal cell. Of the four remaining longitudinal veins the first one is present only in the apical part of the wing (this is the second vein as styled by Hesse, 1956) and is quite evidently the anterior branch of the medius or fourth longitudinal vein, a view amply supported by a study of the wings of *Leylaiya* Eflatoun and *Empidideicus* Becker. This evanescent vein is clearly part of the non-remigial portion of the wing and is being lost by basal rather than distal atrophy. The next vein present in *Dolipteryx* Hesse is, as I interpret it, the anterior branch of the fifth vein and it, too, is evanescent basally. The last heavy vein is the last branch of the fifth vein and the sixth vein is transparent, the anal cell left widely open. The discal cell and second basal cell are completely wanting. The genus differs further from *Empidideicus* Becker in the presence of a deeper, more conspicuous indentation along the anterior eye margin adjacent to the antenna and having the anterior ocelli placed more to the front, besides hypopygial distinctions described below.

Dolipteryx Hesse is based upon 2 species from South Africa.

Length: 1.5 to 2.0 mm., of wing 1.25 to 1.6 mm.

Head, lateral aspect: Decumbent or lower than mesonotum, and rather similar to *Empidideicus* Becker. The occiput is well developed both above and below but is strongly rounded in lateral profile. It lacks a central groove and it is broad on the sides posteriorly so much that Hesse felt that the eyes appeared shifted forward. The eyes are nearly twice as high as wide and they have a much deeper indentation opposite the antennae than in related genera. The proboscis varies in this genus from short and stout to much longer and more slender, being fully 1 mm. long in *nigrescens* Hesse, the body itself only 1.5 mm. The antennae are attached near or just below the upper third of the head. The first segment is quite short and scarcely discernible; the second segment is twice as long as the first and much broader, especially toward the rounded apex; the third segment is about 4 times as long as the first two segments com-

bined, widest basally and there not quite twice as wide as the basal segments; this third segment is strongly attenuate and has a distinct, rather thick, spine tipped, bristly pilose microsegment. The pubescence ventrally on the third segment is more spinulose. The face is rather long vertically, nearly equal to frontoantennal length; the oragenal part of the face is not quite at right angles to face, contrary to the statement of Hesse, and with a few fine hairs on the inside below the face.

Head, anterior aspect: The front converges anteriorly. The eyes are broadly separated above and equally separated in both sexes. The anterior ocellus lies nearer to the front than in *Empidideicus* Becker; eyes separated by a space as wide as posterior pair of ocelli or slightly more. The front has a linear depression running from ocellus to antennae.

Thorax: High and arched, with the head drooping, the pile moderately abundant but composed of such minute, short setae as to require considerable magnification for study. There are a few slightly longer hairs on humeri, on wing bases and sides of scutellum; pleuron bare. Scutellum quite thick, as long as wide, with fine, moderately long, subappressed black setae.

Legs: All of the femora are distinctly a little thickened; on the hind femur the swelling is entirely dorsal. The tibiae are slender. The legs bear very sparse, fine pubescence, a little more dense and distinct on the tibiae which have no distinct bristles or spicules; apical spurs minute. The tarsi are as long as the tibiae, the hind basitarsus unmodified in males. The claws are small and distinct, curved apically, the pulvilli distinct.

Wings: Greatly reduced, and as Hesse notes, quite unlike Bombyliidae. Nevertheless, if compared with the wings of *Empidideicus* Becker, *Leylaiya* Eflatoun, or *Glbellula* Bezzi, the relationship is clear. The second vein ends in the first vein, as in other Mythicomyiinae, the first branch of the medius ends at the midpoint of the apex of the wing and the basal half of this vein has disappeared. There are 3 branches to the medius and 3 to the radius. The sixth is evanescent but the anal cell is widely open. There is no discal cell and there is only one basal cell, the first being present, the others wanting. The axillary lobe is moderately broad only, the alula and ambient vein wanting.

Abdomen: Short and obtuse. There are 8 tergites with the eighth extremely short dorsally and a little longer laterally. The pile of the abdomen is minute and appressed. The apical angle on each side of last sternite in male is extended inward as a spinelike process. Hypopygium of male minute, made of 2 shell-like basimeres, as in other bee flies, but ending apically in a pointed apical process instead of beaked apical distimeres; each is provided on the lower side with a minute hook.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of known male minute, composed of two shell-like basal parts as in the other genera, ending apically in a

pointed apical process instead of beaked apical joints, each provided on inner lower side with a minute hook; aedeagal structure, such as the aedeagus and lateral struts, were not discernible after preparation by boiling in dilute NaOH and these have either been destroyed by the NaOH or are composed of easily soluble structures; the basally directed flattened rod on each side is shown in position; the transverse structures shown at base of the apical processes probably represent part of the lateral rami, the aedeagal complex in the natural state probably just ventral to or associated with them; basal strut small, shown from ventral view and from side with its dorsal process blunt.

Material studied: The types of *crocea* Hesse in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Hesse notes both species were found in the small white blossoms of a species of *Mesembryanthemum*.

Distribution: Ethiopian. *Dolipteryx crocea* Hesse, 1956; *nigrescens* Hesse, 1956.

Genus *Pseudoglabellula* Hesse

FIGURE 345

Pseudoglabellula Hesse, Ann. South African Mus., pt. 6, vol. 50, p. 118, 1967. Type of genus: *Pseudoglabellula meridionalis* Hesse, 1967.

Minute flies, the second basal cell is distinct and distinctly separated from both discal and second basal cells; only 3 veins proceed from the second basal cell. They are readily distinguished from *Glabellula* Bezzi and related genera by the much more narrow first posterior cell which is also narrowed apically and opens into the costa above the apex of the wing. The fourth vein divides into 2 branches leaving a wide, triangular second posterior, apical cell. Hesse (1967) notes that there is no projecting pronotal lobe.

The flies are found in the Koup Karoo District of South Africa.

Length: 1.8 mm.; of wing 1.68 mm.

Just as the present work was ready to be submitted for publication, I received Dr. Hesse's paper describing 3 remarkable new genera of bee flies from South Africa. I quote his description:

A female specimen from the Koup Karoo in the collections before me and which was obtained together with other insects by sweeping flowering shrubs, cannot be allocated to any of the known genera of Cyrtosiniinae [Platypyginae]. It appears to represent a new and as yet undescribed genus. Certain wing-characters seem to suggest a relationship to the genus *Glabellula* Bezzi, but in most of the other venational characters it shows even closer affinity with the genus *Euanthobates*. If the presence of a distinct, though much reduced, marginal cell be taken as a group character, it is referable to the group of Cyrtosiniinae [Platypyginae] genera, such as *Cyrtostia*, *Platypygus*, *Cyrtisiopsis*, *Ceratolaemus* and *Glabellula*, in which a marginal cell is present in the wings, even though sometimes much reduced. On the other hand the rest of its wing-characters, as well as certain antennal and cephalic characters, place it in close proximity to *Euanthobates*.

By comparing it with the descriptions and illustrations of species of the Palearctic *Glabellula*, which also has a similarly

reduced marginal cell, its wings, like those of *Euanthobates*, differ in having the first basal cell distinctly very much longer than the second, and this second basal cell is apparently not formed by the fusion of a discoidal and a second basal cell as is suggested in the case of *Glabellula*; only 3 longitudinal veins, not 4, radiate out from this second basal cell; the 4 posterior cells not formed directly by these delimiting longitudinal veins, but the fourth vein bifurcates into two branches, forming the elongate triangular second posterior cell; first posterior cell, unlike that of *Glabellula*, distinctly very much and markedly narrower and narrowed apically, as in *Euanthobates*, to open on anterior or costal margin and not on apical part of it or very near apex of wing as in *Glabellula*; triangular marginal cell comparatively larger than in *Glabellula*.

Other characters which also distinguish it from *Glabellula* are the markedly short face, the great reduction of antennal joint 4, which is minute, scarcely perceptible as in *Euanthobates*, and not elongate, slender or even rod-like, and the distinctly less convexly humped thorax.

From *Euanthobates*, to which it is generically very closely related and with which it shares such wing-characters as the much narrowed first posterior cell, the very short part of fourth vein before base of second posterior cell, and cephalic characters such as the very short face, and much reduced antennal joint 4, it however differs in having a distinct, reduced, triangular marginal cell present, a very much shorter first posterior cell which curves anteriorly, opening on anterior costal margin at a much longer distance before apex of wings, thus reducing the length of the combined marginal and submarginal cells; a much narrower, more parallel-sided anal cell, more like that of *Glabellula*; a very much broader frons, and even shorter face; much larger antennal sockets; comparatively shorter and broader, truncated, vertical, anterior part of head, with the buccal cavity directed more obliquely forward; and the head below broadly hollowed out or excavated, without a well-defined or delimited, central sulcus.

In other characters, such as the absence of a projecting pronotal lobe, it agrees with *Glabellula*, *Empidideicus* and *Euanthobates*, and differs from *Cyrtosia*, *Platypygus*, and *Ceratolaemus* where this lobe is present.

Material available for study: None; this fly was described by Dr. Hesse whole this work was undergoing final steps for completion. I have republished Dr. Hesse's description and figure.

Immature stages: Unknown.

Ecology and behavior of adults: Flies taken while sweeping over flowering shrubs.

Distribution: Ethiopian: *Pseudoglabellula meridionalis* Hesse, 1967.

Genus *Empidideicus* Becker

FIGURES 107, 108, 328, 348, 591, 594

Empidideicus Becker, Zeitschr. syst. Hymen. Dipt. Tschendorf, vol. 7, p. 97, 1907. Type of genus: *Empidideicus carthaginiensis* Becker, 1907, by monotypy.

Cyrtoides Engel, Die Fliegen der palaearktischen Region, vol. 25, p. 100, 1933. Type of subgenus: *Cyrtoides efflatouni* Engel, 1933, by original designation.

Cladella, new subgenus. Type of subgenus: *Empidideicus propleuralis* Melander, 1946.

Engel (1933), p. 101, key to 3 Palearctic species.

Hesse (1938), pp. 981-982, key to 4 South African species.

Efflatoun (1945), p. 26, key to 3 species from Egypt.

Melander (1946), p. 455, key to 3 species from the southwestern United States.

Very minute, largely black flies with subglobular head, humpbacked mesonotum and stubby abdomen. The proboscis is either very short or in some species even longer than the head. *Empidideicus* Becker is one of several genera, which while having the third vein unforked, likewise have the second vein absent. The vein separating first and second basal cells may be sometimes thinned or evanescent and the discal cell is absent, being confluent with the third posterior cell. There are 4 posterior cells. The anal cell is widely open, the alula wanting as well as the ambient vein. The wing while broad is not so wide as in *Glabellula* Bezzi. *Cyrtosides* Engel is to be distinguished from *Empidideicus* Becker only because the three ocelli are lined up within a straight or nearly straight transverse row. In the related genus *Anomaloptilus* Hesse the discal cell is complete.

Leylariya Efllatoun is readily distinguished from *Empidideicus* Becker because the anterior branch of the medius in addition to being thrust forward is very weak; its anal cell is closed in the margin. The style of the third antennal segment, well developed; in *Empidideicus* Becker is almost totally wanting.

The species *propleuralis* Melander was placed within *Empidideicus* Becker by Melander but he observed that its relationship was probably closer to *Mythicomymia* Coquillett. I believe this is correct and I transfer it to a new subgenus under *Mythicomymia* Coquillett.

Empidideicus Becker is found along the northern coast of Africa and in or near the Mojave Desert of southern California in the United States. Species characters have to do mostly with coloration and shape and proportion of the segments of the antenna.

Length, in type-species: 0.9 to 1.5 mm., of proboscis 0.25 to 0.45 mm., wing expanse 2.5 to 3.15 mm. of larger species, body 1.6 mm. to 2.1 mm., proboscis 0.4 to 0.6 mm., and wing breadth 3.5 to 4.0 mm.

Head, lateral aspect: The head is globular with the occiput very strongly developed, swollen and convex posteriorly. It is thinly pollinose and has a few fine, scattered, bristly hairs. The front is a little swollen with 3 or 4 slender, bristly hairs of no great length in a vertical row on each side of the front and with a triangular depression in front of the antennae. The vertex is strongly swollen; the ocelli are quite large and between the ocelli there are 2 or 3 slightly stronger, pale bristles of no great length. The face and front are quite pale yellow in contrast to the black occiput. The face is short and rather long vertically, moderately becoming a little more prominent at the dorsal border of the orabuccal cavity, and there are 2 distinct bristles at the bottom of the face where the buccal cavity begins. Sides of the oragenal cavity very thin, vertical, and while not extensive beyond the eye they are of about the same extent throughout and back to the posterior corner of the eye. The eye is small, the posterior margin is as convex as the anterior margin.

The proboscis is short, very stout, and robust and in an American species extended obliquely forward and

downward; in length it is a little more than half as long as the head. The labellum bears conspicuous, ventral, bristly hairs. In European species the proboscis is much shorter and stublike, though held in the same position. The antennae are attached at or below the middle of the head in *humeralis* Melander, and above the middle of the head in European species; also, the proboscis is extraordinarily long and slender in the type-species and in the species *mariouti* Efllatoun and is thrust more or less straight downward. The palpus is apparently absent, but dissected material might show a vestige of it. The antennae arise adjacent, the first segment is extremely short and the second segment likewise short, both of these segments are pale with at most minute setae apically, and the third segment of *humeralis* Melander is cylindrical, about the same width as the second segment or barely more narrow and about $2\frac{1}{2}$ times as long as wide. It is micropubescent and bears at the apex a conical microsegment, sharply pointed, also with long micropubescent. In the European species the third segment is rather larger than the second segment, swollen and pyriform or long oval, with long stylelike microsegment.

Head, anterior aspect: From the anterior aspect the front shows a deep, large, triangular pocket or depression in the female. The ocellar triangle is large and obtuse and the front widens toward the vertex, instead of converging. The eyes are widely separated in both sexes. The antennae arise nearly adjacent, the oragenal recess is placed anteroventrally, is rather small and rectangular, and quite deep. It is barely sufficient to emit the large, fleshy proboscis.

Thorax: The thorax is short and compact, the mesonotum moderately humped and convex, less so than in *Cyrtosia* Perris, but more strongly humped than in *Leylariya* Efllatoun; it is a little more steep anteriorly than behind. The mesonotum is generally blackish, sometimes vittate with the lateral margins and sometimes prescutellar area pale yellow. The surface is covered with quite microscopic, rounded scales. There are a few erect, scattered, fine bristly hairs on the surface of the mesonotum, including the humerus, the notopleuron, and the postalar callosity. Whole pleuron with pollenlike microscopic scales similar to those of the mesonotum, but otherwise without pile, except on the propleuron and upper mesopleuron, which bears a few long, scattered, fine hairs. The scutellum is somewhat triangular with rounded apex, either shining black or yellow with micropubescent along the margin, the disc feebly pollinose and disc and margin with a few scattered, moderately long, stiff hairs, 10 or 12 on each side. Halteres quite large proportionately on both the stalk and the club; squama very short. The metasternum is short and more or less covered by the broad attachment of the abdomen; the pronotum is also greatly reduced.

Legs: The legs are comparatively short; the anterior femur is distinctly swollen, a little more so toward the base; middle femur slightly swollen; hind femur stout but not as wide as the middle one. All the femora have

a few fine, stiff hairs more particularly below and more of them near the base. Dorsally there are a few fine, appressed hairs near the apex. The middle coxae are shorter than the others; whole legs mostly yellowish, the femora sometimes brown and the tarsi often blackish on the terminal segments. The tibiae are slender and bear numerous, subappressed setae, the dorsal row on the anterior tibia has about 12 or more elements in it. Claws slender, sharp, curved at the apex, the pulvilli large, the tarsi short, the last segment appears to be scooped out below.

Wings: The wings are short and broad, the veins rather stout, except the branches of the medius which are weaker. The auxiliary vein is atrophied distally, the end of this vein being free in the middle of the costal cell. The first vein R_1 is stout and strong entering the costa near the middle of the wing. The radial sector is also equally stout and so is its continuation, which is all that remains of the radius. This may be regarded as the third vein. It is unbranched and the second vein (R_2+R_3) may be considered to be completely lost. The discal cell is absent due to the loss of the posterior crossvein. The anterior crossvein is quite basal in position, its position nearer the base of the wing than the end of the first vein: vein separating the first and second basal cells atrophied. There is generally a trace of it basally but it is otherwise extremely weak and hardly detectable. The first branch of the medius is forked. There are 4 posterior cells, the first anal vein is barely indicated, the second one is likewise scarcely distinguishable, so that the first anal cell, while open, can hardly be separated from the axillary lobe. The ambient vein is absent and the alula linear or absent.

Abdomen: The abdomen is broad basally, sometimes broader than the thorax, and either ovoid or conical in shape with 6 or 7 apparent segments. Efflatoun (1945) notes that the genitalia are so much concealed in dried specimens that it is often impossible to distinguish between sexes. Generally the abdomen is in large part yellow with black bands basally of varying extent reaching across the tergites but not extending to the sides and laterally with a black punctiform spot on each side of each tergite.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of males with the basal parts small and shell-like; apical process lobe-like or knob-like, having a prominent hook at its base ventrally; aedeagus shortish and tubular; rods on each side of base of aedeagus very prominent and long; lateral struts prominent and well developed; basal strut peculiar in having a medial dorsal apically directed process and also a dorso-ventrally flattened process on each side.

Material available for study: Consists of the series within the National Museum of Natural History, representatives given me by Dr. Melander, and representatives of the type-species received in exchange from Cairo University.

Immature stages: Unknown.

Ecology and behavior of adults: Efflatoun (1945) comments upon their abundance on the inside of flowers, especially desert Compositae and also in the flowers of *Zilla spinosa*, a common desert plant everywhere in Egypt. He also notes that these flies, like *Cyrtosia* Perris, can be captured in great numbers on the inside of desert flowers. Bezzi (1926) comments on the widespread abundance of all the related genera of this group noting that they have been found in India, Australia, Tasmania, Lapland, Cape of Good Hope, and North America.

Distribution: Nearctic: *Empidideicus flavifrons* Melander, 1950; *humeralis* Melander, 1946; *propleuralis* Melander, 1946; *scutellaris* Melander, 1946.

Palaeartic: *Empidideicus carthaginiensis* Becker, 1907; *efflatouni* Engel, 1933 (as subg. *Cyrtoides*); *humgaricus* Thalhhammer, 1911; *insularis* Frey, 1958; *mariouti* Efflatoun, 1945; *nubilus* Bezzi, 1925; *perfectus* Becker, 1910; *serenus* Becker, 1915; *turgestanicus* Parnonov, 1947.

Ethiopian: *Empidideicus beckeri* Bezzi, 1908; *turneri* Hesse, 1938.

Subgenus *Cyrtoides* Engel

Minute, strongly humpbacked flies with short compact abdomen. These flies are very similar to *Empidideicus* Becker and separated from that genus by the alignment of the 3 ocelli into a straight line transversely. *Cyrtoides* Engel is based upon *Empidideicus efflatouni* Engel, which Engel (1933) called a subgenus, and described the species from Egypt and Turkestan. Engel (1933) gave *Cyrtoides* status of subgenus under *Empidideicus* Becker; Efflatoun (1945) made no comment upon it beyond redescribing the species he called abundant in Egypt, but Melander (1946) gave it generic status, which it hardly deserves, and so I have brought it back to subgeneric status inasmuch as, according to Efflatoun (1945), the position or alignment of the ocelli is somewhat variable.

Length: 1.5 to 2.4 mm., wing expanse 2.5 to 4.0 mm.

Distribution: From Egypt and Turkestan.

Genus *Anomaloptilus* Hesse

FIGURES 353, 586, 595

Anomaloptilus Hesse, Ann. South African Mus., vol. 34, p. 983, 1938. Type of genus: *Empidideicus (Anomaloptilus) cellulifer* Hesse, 1938, by original designation.

Minute flies, which as Hesse (1956) notes are almost indistinguishable from *Empidideicus* Becker except in the constant presence of the distinct discal (discoidal) cell. Since the second vein is wanting, both these genera fall within the subfamily Mythicomyiinae as defined by Melander (1946). Hesse (1938) gave *Anomaloptilus* subgeneric status, but Melander in the above-cited paper raised it to generic status, which I believe it certainly deserves. A separate description is hardly necessary.

These flies are found in several localities of the Cape Province of South Africa.

Length: 1.5 to 1.66 mm., of wing 1.2 to 1.66 mm.

Material studied: The types in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic: *Anomaloptilus atomus* Frey, 1958.

Ethiopian: *Anomaloptilus basutoensis* (Hesse), 1967 (as *Empidideicus*); *brevistilus* (Hesse), 1967 (as *Empidideicus*); *cellulifer* (Hesse), 1938 (as *Empidideicus*); *notatus* (Hesse), 1967 (as *Empidideicus*).

Genus *Euanthobates* Hesse

FIGURES 350, 758

Euanthobates Hesse, South African Animal Life, vol. 11, pp. 482-484, 1965. Type of genus: *Euanthobates pectinigulus* Hesse, by original designation.

Acoccus, new subgenus. Type of subgenus: *Euanthobates melivorus* Hesse, 1967.

These are very small flies. They are related to *Empidideicus* Becker and less so the *Cyrtosia* Perris yet are quite different. The body is more plump or stout and the thorax is distinctly less humped and is comparatively broader and has no projecting lobelike pronotum. The wings are similar to *Empidideicus* Becker, and much shorter than the body. With other members of the Platypyginae and *Empidideicus* Becker, it has a groove or sulcus beneath the head. They properly belong in the subfamily Mythicomyiinae, and they show the typical venation of this group.

This flower-feeding species, as in the case of most of the known species of both Mythicomyiinae, Phthiriinae and Platypyginae, has become adapted to an anthophilous habitat. The mobile and apparently protrusible, downwardly directed proboscis, and the remarkable, downwardly projecting, chitinous, caecalike or finger-like processes along the sulcus on the head below are probably adaptations to flower feeding. However, according to Hesse (1967) they are not found among the new species of this genus that he described. These processes, arranged irregularly comblike or brushlike in the gular groove, appear to be unique among known Diptera, if not among insects, and their significance is unknown and can only be guessed at. Their evolutionary origin may be connected with the sulcus or groove below the head that also characterizes other flower-feeding Cyrtosinae, such as the representatives of *Platypygus* Loew, *Cyrtisopsis* Ségué, *Ceratolaemus* Hesse, and *Empidideicus* Becker, and in which they serve to carry out some unknown and specialized function. These structures do not appear to be connected anatomically with the proboscis, labella, or labrum as are the outgrowths or "pseudotracheal processes" of some other flower-feeding Diptera, such as are found, among others, in representatives of the tabanid genus

Philoliche Austen.

These flies are from the Kaokoveld area of South West Africa.

Length: 1.6 to 2.04 mm.; of wing 1.16 to 1.4 mm.

Since I have not seen material of this genus I quote Hesse's (1965) description of this genus and comparison with other genera. To the genera cited I have added author's name.

Head perpendicularly truncate in front as in *Empidideicus* Becker, slightly more spherical, but the eyes also situated slightly forward; frons slightly depressed, slightly broader basally than apically; face however markedly short, very much shorter, relative to frontal length, than in either of the other two genera, the antennae thus situated far forwards; antennae differing from those of both *Empidideicus* Becker and *Cyrtosia* Perris in having the third joint more elongate, leaf-shaped or spear-blade-shaped, flattened, ending apically in a minute (not elongate), scarcely perceptible, terminal element, but with joints 1 and 2 however also short as in the other two genera; buccal cavity below the head anteriorly as in *Empidideicus* Becker, not terminal as in *Cyrtosia* Perris; proboscis as in former, with relatively short and stoutish labral part, protrusible, much more so than in *Empidideicus* Becker, and comparatively long; head below grooved or sulcate, the sulcus in this species with remarkable, downwardly-projecting, finger-like, caeca-like or strap-like processes, arranged irregularly comb-like along the sulcus.

Wings as in *Empidideicus* Becker, also much shorter than body, but with the first basal cell distinctly much longer than second; first posterior cell markedly narrow, narrowed apically, and narrowly open on apical margin of wings, its lower or posterior vein thus ending at or before apex of wings, not posterior to it; part of vein between first basal and second posterior cells markedly short, considerably shorter than in *Empidideicus* Becker; anal cell comparatively broad, broader than in latter genus, narrowed apically; alula narrow or wanting as in *Empidideicus* Becker. Vestiture fine and very short, but apparently denser and shorter than in latter genus, especially on the abdomen.

This peculiar species, of which the representatives are unfortunately preserved in alcohol and have thus become distended and discoloured, is characterized as follows:

Body (as far as can be seen in the preserved specimens) very dark, blackish brown; facial part in front more yellowish; eyes reddish to reddish brown; sides of thorax above and hinder part of border of scutellum reddish brownish; pleurae mainly reddish brown; abdomen above yellowish brownish to mainly dark, dark blackish brownish, with the hind margins of tergites only narrowly, or scarcely, paler and more yellowish, not extensively pale on sides; venter pale or yellowish; femora reddish brownish, their extreme apices more yellowish; tibiae and tarsi more yellowish, but apical parts of tarsi darkened.

Vestiture with the hairs minute, pale.

Head with antennal joint 3 slightly elongate, flattened, spear-blade-shaped or leaf-shaped, broadest nearer base, about three times as long as broad; proboscis with the short, stoutish, labral part about 0.16-0.2 mm. long, the extruded proboscis itself pale, slender, rather soft, much longer than entire body, about 1.14-3.68 mm., its labella small; caeca- or strap-like processes in sulcus below head not all equally long, the longest about 0.16 mm. long, in ventral view appearing slightly broadened strap-like.

Wings slightly, but distinctly, tinted yellowish; veins yellowish; first posterior cell markedly narrowed apically; anal cell narrowed apically, but still distinctly open.

Material available for study: The University of Lund lent me specimens of this genus.

Immature stages: Unknown.

Ecology and behavior of adults: "Found on yellow composites near Welwitschia."

Distribution: Ethiopian: *Euanthobates mellivorus* Hesse, 1967; *pectinigulus* Hesse, 1965.

Genus *Leylaiya* Eflatoun

FIGURE 346

Leylaiya Eflatoun, Bull. Soc. Fouad I^{er} d'Ent., p. 21, 1945. Type of genus: *Leylaiya minnermia* Eflatoun, 1945, by original designation.

Minute flies, less deeply humped than in either *Empidideicus* Becker or *Cyrtosia* Perris. They are usually entirely orange yellow, except rarely with thorax or third antennal segment obscured by dark brown. They are quickly distinguished from *Empidideicus* Becker by the fact that the style of the third antennal segment is so minute as to be almost nonexistent, and the anterior branch of the medius is so weak that it is nearly effaced and moreover is rather strongly thrust forward. Like *Empidideicus* Becker the auxiliary vein is vestigial distally, the radial sector is unbranched, and the first vein ends in the middle of the wing. Alula, and ambient vein and discal cell are all absent and the anal cell is closed in the margin of the wing.

These curious little flies are known from a single species captured in two desert wadies of Egypt only some 50 kilometers apart.

Length: 1.1 to 1.3 mm., of proboscis 0.1 to 0.5 mm., wing expanse 2.8 to 3.2 mm.

As I have not seen any material of *Leylaiya* Eflatoun, I quote his description:

Head remarkably elongate and somewhat pyriform when seen from above, narrower or much narrower than the thorax and distinctly longer than broad; the head is rounded behind, owing to the very puffed-out and bulging occiput (even more so than in *Cyrtosia* Perris) and then produced forward cone-shaped and gradually narrowing down beak-like apically where it terminates by the short and comparatively stout proboscis; frons a little broader above than below (at the base of the antennae) and narrower in the male than in the female; face short but conspicuously produced vertically upwards below, in a short hump-shaped projection (which is the upper border of the mouth-margin), consequently the very short face itself appears deeply concave, almost semi-circular; from this hump-shaped projection the correct mouth-margin slopes perpendicularly downwards, almost at right angles with the face and frons; genae very narrow, linear; proboscis short, rather stout and about as long as the length of the head (twice as long as the entire mouth-margin).

The palpi are apparently absent; vertex broad and the broad triangle formed by the ocelli (ocellar tubercle) is hardly approximated at the base that they touch, as in *Empidideicus* Becker and *Cyrtosia* Perris and consist of a very short, rounded basal segment, a short cylindrical second segment (about twice as long at the first, as in *Empidideicus* Becker), and a long, broad, pear-shaped third segment whose apical style is so minute (hardly visible even under high magnification) that it may be termed absent.

Material available for study: None. I have quoted the description of Eflatoun.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian (Egypt): *Leylaiya minnermia* Eflatoun, 1945.

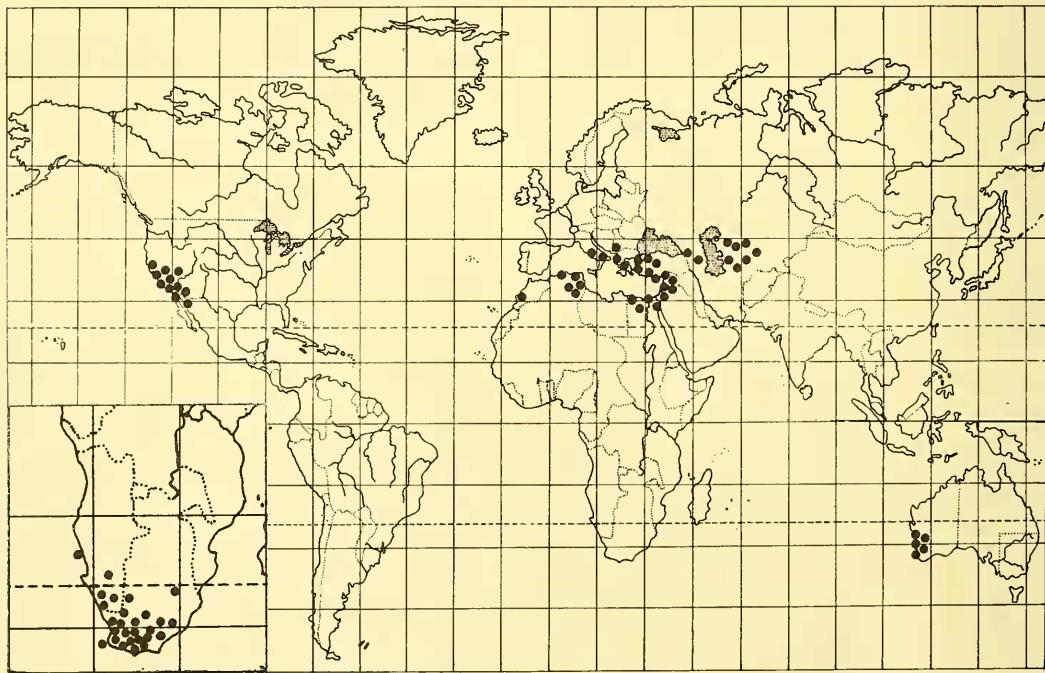
Division TOMOPHTHALMAE

Subfamily Cylleniinae Becker, 1912

This small subfamily contains some remarkable and interesting and unusual bee flies. They are at once characterized by: (1) the deeply cupulate recess within the posterior occiput with its marginal fringe of hair about the rim. (2) The plane, or birectiform, posterior eye margin not indented or bisected either. Generally the antennae and proboscis are elongate, but the former are short within the tribe *Tomomyzini*. (3) The second vein arises basal to the discal cell and arises at an acute angle. The nonindented and nonbisected postmargin of the eye and the place and manner of origin of the second vein separates this subfamily from the Lomatiinae.

After a lengthy and comprehensive study of some sixty characters in almost all of the genera of the two subfamilies, I find these to be the only consistently divisive characters. In fact the two subfamilies are so closely allied they might almost be combined into one with a series of tribes. All included genera have the metanotum bare, except *Peringueyimyia* Bigot. A pilose metanotum is a distinguishing characteristic of the Lomatiinae and it is possible that *Peringueyimyia* Bigot belongs there. This subfamily is almost restricted to the Palaearctic and Ethiopian regions. The unique genus *Neosardus* Roberts is Australian, and so is

CYLLENIINAE



TEXT-FIGURE 41.—Pattern of the approximate world distribution of the species of the subfamily Cylleniinae.

Docidomyia White. Only *Paracosmus* Osten Sacken and its close allies are found in the Nearctic region. Nothing is known concerning the life histories in this subfamily; Bezzi, in Latin, described the pupa of *Cyl- lenia marginata* without comment as to host. Since many of these flies are commonly found resting upon soil it may be surmised that the hosts are subterranean. The *Henica* Macquart and *Neosardus* Roberts groups both have a well-marked row of acanthophorite spines on each side of the ovipositor much as in soil-ovipositing asilids.

It is my belief that the genus *Eclimus* Loew and allied genera, as *Thevenemyia* Bigot (*Ecliminae* of Hall, 1969), find their proper relationship within the Bombyliinae where I place them as a special tribal subdivision. I quite concur with Mr. Hall that it deserves special rank. Within the Cylleniinae my studies convince me that I must recognize the following division:

Tribe Cylleniini

This tribe is characterized by thorax and abdomen with strong bristles. The third antennal segment with small bristles especially at apex. Proboscis and antennae varying from long to short. Metapleuron and metanotum bare except for micropubesence. Contains *Cyl- lenia* Latreille, *Amictus* Wiedemann, and *Sinaia* Becker, and also *Sphenoidoptera* Williston.

Tribe Henicini

(Heniconiinae of Hall, 1969.) Characterized by occipital lobes shallow but narrowly separated; the antennae are long and the proboscis is long; especially characterized by the virtual absence of the metanotum; the abdomen and thorax are so closely jammed that the metanotum is almost obliterated; both metapleuron and metanotum without pile. Included are *Henica* Macquart and *Nomalonia* Rondani.

Tribe Tomomyzini

(Tomomyzinae of Becker, 1913.) Characterized by the projecting face that extends at least beyond the

antenna; the face is relatively short but conical and oblique. The ocelli are set far forward from the posterior corner of the eye. The antennae are short and the proboscis is confined to the oral cavity; the condition of the metapleuron and metanotum varies; of the six included genera all have the metanotum bare except *Tomomyza* Wiedemann where it is either pilose or bare; all have the metapleuron pilose; *Tomomyza* Wiedemann has pile on the upper hypopleuron and has a plumula; it should possibly be placed in a separate tribe. Included are: *Paracosmus* Osten Sacken, *Meta- cosmus* Coquillett, *Amphicosmus* Coquillett, *Panto- stomus* Bezzi, *Docidomyia* White, *Tomomyza* Wiede- mann, and *Aetherosia*, new subgenus. Several South African species formerly placed in *Tomomyza* Wiede- mann belong in *Paracosmus* Osten Sacken.

Peringueyimyini, new tribe

In this tribe I place the single genus *Peringueyimyia* Bigot. It is peculiar. It appears to have all of the characteristics of the Lomatiinae except the indented or bisected post eye margin. The occiput is extraordinarily thick, antennae rather elongate and slender, and the genae are prominent and deeply shelving inward; with the dense long pile beneath the third antennal segment they are much like the Comptosini. The metanotum in front of the haltere is without pile but the metanotum is densely pilose.

Neosardini, new tribe

Here I place the unique genus *Neosardus* Roberts. It has the general characters of the subfamily. The anten- nae and proboscis are both long and slender. Especially to be noted is the extraordinarily wide face and very wide gena. The occipital cup is present though per- haps smaller, the occipital lobes wide, widely separated and shallow. Both metapleuron and metanotum with- out pile.

KEY TO THE GENERA AND SUBGENERA OF CYLLENIINAE

1. Genofacial space extraordinarily wide, especially the genae. Front also very broad in females. Males dichoptic. Four submarginal cells present and wing with an *Euxoprosopa*-like pattern. Antenna elongate and cylindrical and all three segments conspicuously and densely appressed setate; first antennal segment as long as the third or even longer; last segment tapers sharply from the base and ends acuminate with a minute, bristle-tipped microseg- ment. *Neosardus* Roberts
Genofacial space scarcely more than one-third the head width and often much less. Antennae shorter, differently

- shaped and proportioned. Usually 2 and never more than 3 submarginal cells present 2
2. Thorax, scutellum, hind tibiae, and sometimes the abdom- inal tergites with strong, long, conspicuous bristles . . 3
Rather small flies of 4 to 10 millimeters length and often with relatively slender, moderately elongate abdomen. Comparatively bare flies with or without areas of dense, always short, fine or bristly, erect or appressed pile. No strong bristles present anywhere 9
3. Large, robust flies with semidecumbent head and drooping abdomen which bears appressed coarse hair and on the

postmargins of the tergites only appressed rather short, bristly hairs. Femora and tibiae with conspicuous, spine-like bristles. Notopleural and supralaral bristles strong. First antennal segment much swollen with dense downwardly directed pile below and subappressed bristly pile above. Third antennal segment as long as the first, strongly tapered and narrowed. There are 2 submarginal cells; anterior branch of third vein arising as a crossvein with long backward spur; wing hyaline; end of marginal cell bulbous below at apex; first posterior cell closed. Occiput very extensive, lobes tightly apposed.

Peringueyimyia Bezzi

Not such flies. First antennal segment both elongate and heavily swollen. Scutellum with strong bristles 4

4. Postmargins of the tergites with conspicuous, long, erect bristles. Frons depressed and usually with a distinct, medial groove 5

Postmargins of tergites and whole surface with only dense, appressed scalliform pile. Frons elevated, swollen, smooth. First antennal segment short and round, globose. Occipital lobes widely separated. Metanotum almost completely reduced 8

5. Proboscis long and slender, usually much longer than the head; if shortened and scarcely longer than head the wing is hyaline. Antennae comparatively slender and elongate. Flies often brownish yellow in color, vittate thorax, and elongate, cylindroid, distally compressed abdomen. Wings almost always hyaline 7

Proboscis relatively short scarcely as long as head and often shorter. Antennae also rather short; apex of the short-ovate, flattened third antennal segment with a few, slender bristles especially near the apex. Flies rather small, black, the abdomen of moderate length, rather flattened, as wide as mesonotum and with dense, appressed scalliform pile in addition to bristles. Wings with axillary lobe much narrowed, especially toward the base. Wings always with a blackish border or pattern of scattered black or brown spots that may be faint. Intercalary vein plane, usually rectangular to the fourth vein 6

6. Oragenal cup rather extensive both above beneath the antenna and below along the sides, and polished and bare, and convexly rounded outward along its walls; no bristles or pile present upon it. Intercalary vein forms a right angle with fourth vein above. Two submarginal cells. Frons beset with rather long, stiff, erect hairs.

Sphenoidoptera Williston

Oragenal cup very short and with several long, conspicuous, stout bristles and bristly hairs on each side just below the antenna. Frons densely beset with long, erect, bristles. Three submarginal cells and intercalary vein set at an angle. Narrow genae pollinose and not vertically shelving inward along eye margin. *Cyllenia Latreille*

7. Face quite short, but high, the oral opening reaching only a short distance above the proboscis. Antenna rather like *Amictus* Wiedemann, but a little less slender and the proboscis distinctly shorter and stouter, not much if any longer than the head, and labellum stouter. Wing hyaline, with 2 submarginal cells and all the posterior cells and anal cell widely open. Occiput in profile quite extensive on the upper half of head. *Sinaia Becker*

Face longer, subconical, distinctly and triangularly peaked forward. Proboscis 2 to 4 times as long as head and together with labellum quite slender. Upper occiput moderately or not at all developed; occiput relatively shallow with the upper lobes separated. First posterior cell open or closed. Submarginal cells usually 2 in number, rarely 3. Wing almost always hyaline; never with conspicuous markings. Males sometimes with curious, very long apical bristles on first tarsal segments. Some males with a double row of short, close-set spines upon lower surface of middle tarsi . . . *Amictus Wiedemann*

8. Marginal cell divided into 3 parts by crossvein. Frons with numerous stiff bristles. *Hemica Macquart*
Marginal cell simple, without crossveins. Frons with a few stiff hairs *Nomalonia Rondani*

9. Marginal cell at apex simple and not swollen or widened even in forms that have 3 submarginal cells. Wing hyaline. Flies with rather long and slender abdomen. Hind femur with a few fine hairs below 10

Marginal cell distinctly widened at apex and bulbous, protrusive, widened, and rarely even with a radial loop or ending bluntly with the terminal section of the second vein plane 11

10. Three submarginal cells *Amphicosmus Coquillett*
Two submarginal cells *Metacosmus Coquillett*

11. Wing hyaline with a conspicuous long radial loop; second submarginal cell long and slender and arising as an arch or as crossvein with long backward spur. Eye exceptionally large leaving genofacial and oral area reduced, proboscis very short and muscoidlike. Eyes of male narrowly separated by a long, parallel-sided space, the ocelli set very far forward; slender, compressed, often annulate abdomen and prominent male terminalia much as in *Paracosmus* Osten Sacken. Metanotum bare, hind femur scanty, long erect hairs below . . . *Dicidomyia White*
Not such flies 12

12. Three submarginal cells. Anterior part of wing on basal two-thirds yellowish brown. Anterior branch of third vein arising plane and obliquely. Abdomen club-shaped apically. Whole surface of hind femur densely covered with comparatively long, distinctly appressed, stiff hairs. Marginal cell wider apically than before the crossvein, but ending plane of genus. Rather large species 12 or 13 mm. in length.

Not such flies 13

13. Wing water clear, the veins yellow. Face scarcely at all produced beyond the antennal insertion. Third antennal segment rather elongate, narrowed basally, dilated apically. Marginal cell dilated or swollen below but ending truncate. Whole insect quite pale yellow or yellowish red except middle of mesonotum and sternum. Abdomen cylindroid but stout, not compressed, basally as wide as mesonotum. Pile very fine, dense, appressed and setate. Ocelli vestigial or reduced. A punctate depression in the middle of frons in front of ocelli.

Paracosmus (Aethrosia, new subgenus)

Not such flies 14

14. Abdomen slender, compressed laterally, the male terminalia large, protuberant. Abdominal pile very fine, appressed, dense, setate, without any tufts of longer pile in the middle; postmargins of tergites with yellow or white borders widened medially. Frons concave and smooth and without any elevations either toward vertex or on each side of antennal basal base; surface silvery gray pollinose with a few appressed hairs, either fine or bristly. Wing hyaline; 2 submarginal cells; basal arch of second submarginal cell either rounded, or simulating a crossvein with backward spur *Paracosmus Osten Sacken*
Abdomen comparatively shorter, distinctly wider, rather robust in appearance and always with patches of longer, partly erect, partly curled, and appressed pile lying on each side of the tergites 15

15. Wing with 3 submarginal cells and both second and fourth veins very erratic, and with outward spurs. Wings spotted *Tomomyza Wiedemann*
Wing with 2 or 3 submarginal cells. Wings hyaline or tinged with brown or black 16

16. Two submarginal cells. First antennal segment twice as long as the second and the face below antenna very short, not extending to the end of the first antennal segment. Ocellarium long and unusually high and well developed. Small, often reddish, rather robust flies with the abdo-

men relatively short like *Tomomyza* Wiedemann, and with the posterior margins of the tergites often strongly raised leaving a corrugated aspect and sometimes with concave or foveate depressions on each side. Anterior branch of third vein usually simulating a crossvein and with a backward spur. Hind femur with appressed setae pile *Pantostomus Bezzi*
 Three submarginal cells. First antennal segment quite short; face below antenna extending much beyond the

first antennal segment. Ocellarium raised but rather low and gently raised. Shining black, rather robust flies with abdomen much like the *pictipennis* group of *Tomomyza* Wiedemann. Abdomen without posterior tergal margins strongly raised or lateral foveate depressions. Hind femur with erect or suberect stiff hairs, especially erect and longer below. Venation of second and anterior portion of third vein rather erratic with sharp bends and simulated crossveins *Tomomyza* Wiedemann

Genus *Cyllenia* Latreille

FIGURES 116, 117, 358, 616, 756, 771, 777

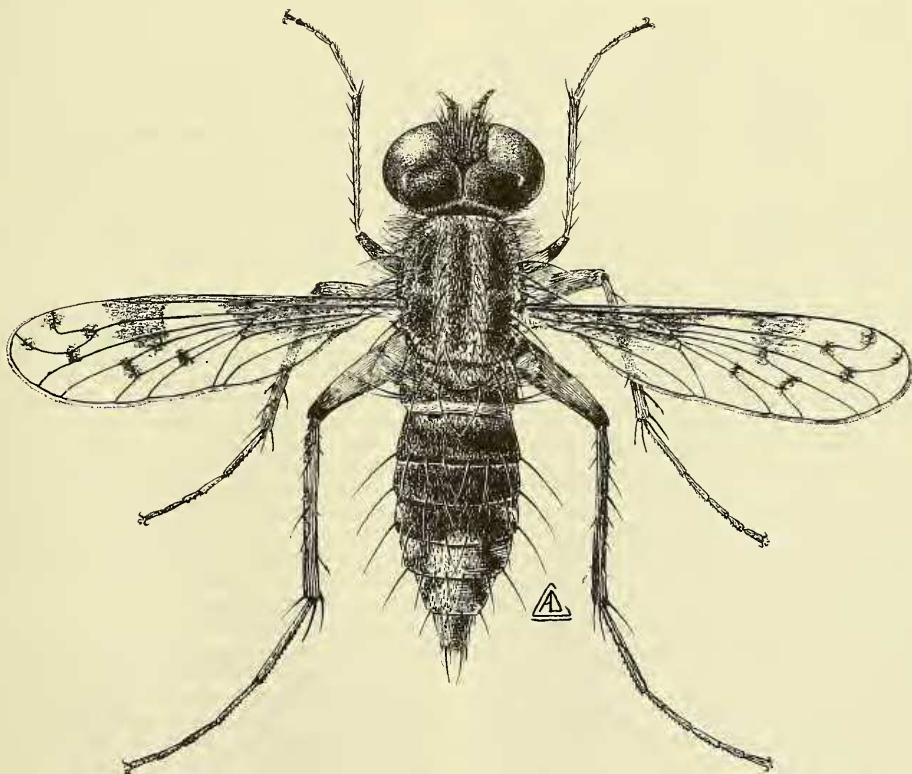
Cyllenia Latreille, Histoire nat. Crustacés Insectes, part 3, p. 429, 1802. Type of genus: *Cyllenia maculata* Latreille, 1802, monotypy.

Engel (1933), p. 11, key to 5 Palaearctic species.

Small flies, distinguished by the subglobular head, a little peaked in front beneath the antenna, the conspicuously swollen occiput and the presence of 3 submarginal

cells in the wing; also, there are strong bristles beneath the hind femur and on the postmargins of the abdominal tergites. The abdomen is somewhat compressed, convex, subcylindrical, and slightly arched or decumbent.

There are other characteristic features. The anal cell is widely open and the third posterior cell arises abruptly and very convexly from the fourth posterior cell; the wing is slender basally, the alula wanting or much reduced; the wing is usually patterned with brown spots more or less sharply demarcated. The occi-



TEXT-FIGURE 42.—Habitus, *Cyllenia maculata* Latreille.

put is strongly bilobate above with a small but deep central cavity; viewed laterally it is conspicuous and wide on the upper two-thirds; posterior vertical margin of eye very slightly concave but without middle indentation or bisecting line. This is the genus upon which the subfamily Cylleninae is founded. The proboscis is stout and of medium length, and the antennae remind one of the Lomatiinae, the laterally compressed and thinned and offset third segment has apical bristles.

Cyllenia Latreille comprises a small group of Palaearctic flies distributed through southern Europe, Turkestan, and Asia Minor.

Length: 3.5 to 8 mm., usually about 5 mm.

Head, lateral aspect: The head is subglobular in shape or even somewhat triangular, partly due to the angular peak of the face extending out nearly to the end of the first antennal segment and partly due to the prominent, extensive occiput, which is especially extensive from the dorsal aspect; the occiput is also bilobate and has a well-developed central epukle recess or cavity. However, the posterior margin of the eye is very slightly concave and there is no medial indentation or bisecting line. The face is only moderately prominent and the peak is almost exactly opposite the midlevel of the head; it bears a conspicuous fringe of slender bristles down the sides of the oragenal cavity, but the face immediately beneath the antennae is bare. The oragenal recess is wide, narrowed above, and the gena is as wide as the basal antennal segment. The palpus is elongate and quite slender and clearly composed of 2 segments; it is nonhairy.

The proboscis is relatively short and stout with large fleshy labellum bearing a number of fine, stiff, erect hairs on its ventral surface. It projects a little beyond the oral cavity and slightly beyond the antenna, but it is not as long as the head. The antennae are attached a little above the middle of the head; they are comparatively short and the first segment is widened distally, bears a few short, fine bristles dorsally and is broadly attached to the second segment; it has rather more bristles ventrally, but they are not numerous nor long. Viewed dorsally the second antennal segment is obliquely subtruncate apically both medially and again laterally; it is to the lateral apex that the third segment is attached; viewed dorsally it has a dense patch of minute setae, some longer ones below. The third segment viewed laterally is stout, except at the immediate apex, which is turned downward, ends truncately, bears an apical spine and 4 or 5 distinct bristles; dorsally there is also a cluster of appressed bristles in the middle of the segment; viewed dorsally it is greatly thinned, becoming attenuate near the base. The third segment is not quite as long as the combined length of the first two segments.

Head, anterior aspect: The eyes in the male are separated at the vertex by a distance not quite twice the width of the ocellar tubercle; the front widens rapidly below. The ocellar tubercle is conspicuous, high, with vertical sides and lobiform. Between the small ocelli there is a tuft of long, coarse hairs. The upper eye has

rounded corners viewed above and is separated from the ocellar tubercle. Viewed above the two sides of the occiput meet behind the ocellarium and leave a deep pocket. The pile of the occiput is dense, except near the eye margin, but short and fine, and directed backward. The eyes are bare. There is almost no development of the head beneath the eyes although the cheeks are moderately wide seen from below. The tentorial groove is deep and ends opposite the upper point of the oral recess. The antennae are attached close to the upper end of the oral recess. Both face and front are pollinose. The face has a preoral fringe of about 9 or 10 moderately long, stout, silvery bristles on each side.

The middle of the front has a large, triangular patch of long, rather dense, coarse hairs; the dorsal pile is black, the lower pile above the antenna is silvery.

Thorax: The thorax is relatively narrow and slightly convex with 5 irregular, indistinct rows of flattened, white scales; also there is a short, abbreviated row of 5 or 6 fine, acrostical, bristly hairs. There are some similar scattered hairs laterally, 2 long, but quite slender, bristles on the notopleuron, 2 above the wing, 2 on the postalar callosity, 3 pairs on the scutellar margin that are rather long, and some shorter hairs, 2 or 3 on each side of the scutellum. The basal half of the disc of the thick, posteriorly convex scutellum is rather densely covered with pale scales, and a line of scales divides a shallow, medial, posterior depression. The humerus has scales and some coarse hairs. The pleuron is relatively bare; there is a horizontal row of rather long, conspicuous, outwardly directed, whitish scales on the mesopleuron culminating in a posterior patch on this sclerite. Above the scales is a row of scattered, fine hairs and a small patch of scattered scales is on the upper part of the sternopleuron, otherwise the pleuron is bare.

Legs: The femora are moderately stout, slightly enlarged through the middle, rather densely covered with whitish scales; tibiae with more scattered similar scales. The hind femur has a conspicuous row of ventromedial, stout, long bristles that give way basally and ventrally to equally long but more bristly hairs. The hind tibiae has 3 rather long, anterodorsal bristles and 2 or 3 similar, posterodorsal bristles and has 1 anteroventral bristle and 2 or 3 setae; apex with 5 bristles, 3 or 4 of which are long and conspicuous. The anterior femur is narrowed distally, a little swollen basally, without bristles but with a ventral row throughout of dense, fine, suberect, very abundant setae; its tibia has 4 or 5 fine, slender, rather short dorsal bristles.

Wings: The wings are hyaline, in most species with rather light brownish spots about the crossveins, and sometimes with a band extending to the costa. There are characteristically 3 submarginal cells, the vein R 4 simulating a crossvein. In the middle the discal cell is strongly occluded from below by the strongly arched base of the third posterior cell; the intercalary vein simulates a crossvein. The anal cell is widely open, the axillary lobe slender, the alula quite narrow or absent.

The anterior crossvein enters the discal cell at the outer fourth; the marginal cell is strongly widened apically.

Abdomen: The abdomen is compressed laterally; only the first segment is as wide as the thorax; the apex of the abdomen is a little widened, and it is convex and slightly recumbent. The posterior margins of the segments on each side have conspicuous, quite long, erect, black bristles, 3 or 4 on each side. Lower down on the sides of the abdomen there is much long hair varying from coarse to fine, white in color and the bristles black. The whole abdomen is covered rather densely with scales, pale in color, or of two colors, mostly white below, mostly light brown above. The lower scales are large, the upper scales narrow and more like flattened hairs. Terminalia with a pair of convex plates closely adjacent, lower corners of the last sternite curved upward and backward as a flap or lobe. Beak of terminalia extended downward.

Material available for study: I am deeply indebted to Dr. R. H. Painter for lending material in this genus.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical: *Cyllenina unicolor* Jaenicke, 1867.

Palearctic: *Cyllenina globiceps* Loew, 1870; *laevis* Bigot, 1888; *maculata* Latreille, 1802 [= *cyllenina* (Lamarek), 1816 (as *Ploas*)]; *marginata* Loew, 1846; *obsoleta* Loew, 1846; *rustica* (Rossi), 1790 (as *Asilus*) [= *maculata* Latreille, 1802]; *turgesitanica* Paramonov, 1929.

Genus *Sphenoidoptera* Williston

FIGURES 235, 364, 601, 610, 1024, 1025, 1026

Sphenoidoptera Williston, *Biologia Centrali-Americana*, Dipt., vol. 1, supplement, p. 295, 1901. Type of genus: *Sphenoidoptera varipennis* Williston, by monotypy.

Small, robust flies with a slightly decumbent head and abdomen, and very large but rather short and wide oral opening which is oblique, leaving the face produced for a short distance beneath the antennae. The proboscis is short, and stout with a large, oval, flattened labella; it is distinctly longer than the antenna and extends beyond it. The head is long with the occiput especially prominent dorsally and becoming quite short along the lower eye margins. Thorax and abdomen and legs with scales. Anterior and posterior tibiae with spines.

The whole sides and middle of the face, both of which are narrow, are bare and the upper occiput is strikingly prominent and produced. The slender wing with narrow axillary lobe, open anal cell and absent alula is suggestive of *Cyllenina marginata* Loew, but in that genus, although the dark pattern in *marginata* Loew is suggestively similar, the shape of the third posterior cell is quite different and there are 3 submarginal cells,

moreover, its face bears a vertical row of distinct bristles.

This genus is known from Mexico.

Length: 7 to 8 mm.

Head, lateral aspect: The face is short, polished, bare, and produced obliquely forward and downward from the antennae for a distance not quite as long as the first antennal segment. At the epistomal margin it is obliquely truncate leaving a large wide opening, at most $1\frac{1}{2}$ times as long as wide, with thin, narrow walls that extend a short distance from the eye margin on the lower portion of the head but not as great as the length of the face. The cheeks form a short triangle posteriorly. Eye prominent without lateral indentation and from the dorsal aspect strongly extended beyond the occiput but only over the lateral and ventral portion of the head. Occiput especially thick and tumid dorsally. The high ocellarium at the vertex lies in a deep fissure, and also between the posterior eye corners, the occiput recedes strongly below. The pile is short, fine and scanty with a few longer, bristly hairs dorsally. The proboscis is slightly widened distally, extended obliquely downward, the terminal lamella large, long, oval, strongly compressed with lateral bristly pile. The palpus is long, quite slender, extending nearly half the length of the proboscis. The antennae are attached at the middle of the head, or moderately elongate and slender; the first segment is nearly 3 times as long as the second, the second segment is short and beadlike; third segment approximately as long as the first and bearing a short, small microsegment beyond which is a second conical microsegment with short, stylate apex.

Head, anterior aspect: The front is wide, only slightly narrowed at the vertex with shallow medial groove, some pollen, and laterally it has numerous, rather long, distinctly bristly, blackish hairs; vertex with 3 or 4 pairs of similar long slender bristles or bristly hairs all lying on the ocellar tubercle behind the ocelli. Slopes of the ocellarium vertical.

Thorax: With scattered, rather short, black, bristly hair, or slender bristles, and similar pile upon the humerus, the lateral margins have rather long, comparatively slender bristles; 2 notopleurals, 2 to 3 supralars, 2 on postalar callosity. There are 2 pairs on scutellar margin with 2 shorter pairs laterally. The thorax is quite convex and thick with a deep crease before scutellum and without pollen or pile. The propleuron has a vertical fringe of scanty, long, stiff pile; the upper half of the mesopleuron bears numerous, rather long, fine bristles or bristly hairs, together with below these bristles a fringe of short, narrow, rather dense, flattened, whitish pile. The sternopleuron, pteropleuron, hypopleuron and metapleuron and the metanotum are all without pile. Ventral metasternum narrow, chitinated, with long, stiff pile. The postmetacoxal area is membranous; squamae without a fringe of pile.

Legs: The hind femur is distinctly thickened chiefly through the middle and beyond and a little compressed laterally. The anterior femur is slightly thickened to-

ward the base. The femora and tibiae, the anterior and posterior coxae all have scales. Hind femur with a rather stout bristle ventrolaterally at the apical fifth; its tibia has 9 dorsomedial, 5 long, stout, and 2 short dorsolateral, 8 mostly shorter ventrolateral and 10 quite short, fine, ventromedial bristles. The anterior femur has a subapical anteroventral bristle; its tibia has 10 posterodorsal, 10 posterior and 9 minute, posterior ventral bristles. Terminal tibial spines strong. Claws short, sharp, curved from the middle and the pulvilli well developed, and with only an exceptionally minute medial lappet.

Wings: Slender, hyaline, with a sharply demarcated blackish pattern of spots and the foreborder blackish to the end of the first vein. There are 2 submarginal cells. The four posterior cells are open, the first posterior cell of uniform width and scarcely wider than the discal cell. The anterior crossvein is situated at the outer third of the discal cell. The anal cell is widely open, the axillary lobe narrow, and while the ambient vein is complete the alula is completely absent. There is a rounded blackish spot at apex of second vein, at base and apex of anterior branch of third vein, on each side of intercalary vein, a band across middle of discal cell widening toward the costa and connected with basal dark border which ends with it; basal to it a clear hyaline area extends to and ends sharply at the second vein.

Abdomen: Broad and robust and longer than wide; it is moderately convex with nearly parallel sides to the end of the fourth segment and with numerous, broad, white scales especially over the middle and posterior margin of the first segment, the basal portions of the remaining segments and with almost as many black scales intermixed. Other pile is very scanty, but the posterior margins of all of the tergites especially laterally have a fringe of quite long, conspicuous, slender, black bristles, which are continued onto the posterior margin of the sternites. Seven tergites present, the seventh is as long or longer than the sixth and strongly compressed laterally, so that its walls are pinched together.

Material available for study: A female of the type-species of the *Biologia Centrali-Americana* material in the British Museum (Natural History). Also, a male given me by my friend, Dr. Rex Painter.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical: *Sphenoidoptera varipennis* Williston, 1901.

Genus *Amictus* Wiedemann

FIGURES 109, 357, 611, 641, 741, 752, 779, 890, 891, 892

Amictus Wiedemann, *Zoologisches Magazin*, vol. 1, pt. 1, p. 58, 1817. Type of genus: *Bombylius oblongus* Fabricius, 1805, by monotypy.

Thlipsomyza Wiedemann, *Nova Dipteriorum Genera*, p. 12, 1820a. Type of genus: *Bombylius compressus* Fabricius, 1805, by monotypy.

Thlypsogaster Rondani, *Arch. Zool. Anat. Fisiol.*, vol. 3, p. 72, 1863. Type of genus: *Thlypsomyza castanea* Macquart, 1840. Rondani had 2 species. Bezzi, p. 4, 1924, gives *T. castanea* as type-species.

Truquia Rondani, *Arch. Zool. Anat. Fisiol.*, vol. 3, (sep.), p. 72, 1863. Type of genus: *Truquia insularis* Rondani, 1863, by original designation.

Thlypsogaster Coquillett, *Trans. American Ent. Soc. Philadelphia*, vol. 21, p. 108, 1894a. Error of identification and lapsus.

Engel (1933), pp. 16-18, key to 21 species.

Austen (1937), p. 78, key to 5 species from Palestine.

Eflatoun (1945), p. 158, key to 5 species from Egypt.

Flies of small or medium size, usually pale pollinose, and readily distinguished by the strong macrochaetae upon thorax, scutellum, and abdomen. The abdomen is narrow, somewhat tapered and either cylindroid or laterally a little compressed. The mesonotum is often vittate. Face nearly bare or with a few, stiff, scattered hairs. The face is rather extensive and extended obliquely forward, the oragenal or buccal cavity sloping obliquely backward, the orafacial angle rectangular. The proboscis is quite long and slender and the antennae are distinctive; the first segment is lengthened, the second beadlike, the third segment moderately elongate with the outer half strongly attenuate, bearing short, stout oblique bristles or setae, its apex with small short, distinct microsegment and bristle. The first posterior cell is open or closed. *Sinaia* Becker is a monotypic genus related to *Amictus* Wiedemann, found in the same region and distinguished by the extraordinarily prominent upper occiput, particularly in the dorsal aspect.

This genus is restricted to the southern Palaearctic region, ranging along North Africa from Morocco to Egypt, the southern border of Europe, numerous in Turkestan and Asia Minor; of 5 species found by Austen in Palestine, 4 were undescribed.

Length: 6 to 11 mm., wings shorter.

Head, lateral aspect: Head hemispherical but with the face rather strongly produced triangularly forward. The occiput is not very extensive but is a little longer dorsally, and, in fact, the occiput is rather flattened and shelves rapidly inward to the margin of the interior cup or recess which, while distinct, is only moderately deep. The fringe on the border of the occipital cup is long, erect, and dense on the upper half, the hairs apparently somewhat scaliform or flattened and with the pile decreasing in length laterally to the eye margin and becoming flat-appressed at the upper eye margin. The front is flat, slightly sunken beneath the eye margin, pollinose, only the lower half bearing some stiff bristly hairs directed forward. Middle of front on the lower half with a deep, medial groove. The face is conically peaked forward, shining and apt to be light yellow or brown with some pollen laterally and with a few bristly hairs of varying lengths never as long as the first antennal segment. In females the entire front may have scattered bristly hairs. The posterior margin of the eye on the upper two-thirds is not quite plane in some

species, more nearly so in others. Upper eye facets of the male enlarged only narrowly near the eye margins.

The proboscis is long and slender, 2 to 3 times the length of the head. The labellum likewise slender. Palps very slender, not extending beyond the oral recess. Antenna attached a little above the middle of the head, moderately long and slender. The first segment is a little wider apically, about 4 times as long as wide, and reaching as far as the apex of the face in most species. This segment bears only a few short appressed setae dorsally. The second segment is short and beadlike. The third segment is as long as the first two segments together, may have a narrow knob at the base, is never wider than the second segment, and is very gradually attenuated on the outer half. It may become quite narrow on the apical third and often bears some short, distinct, bristles medially. Shorter bristles may extend dorsally nearly to the base. Apically there are 2 very small beadlike microsegments with a bristle at the tip of the last one.

Head, anterior aspect: From the anterior view the head is almost circular; the eyes are distinctly separated in the males by a distance a little greater than the ocellar tubercle, and, perhaps, nearly equal to twice the width of the second antennal segment. The front at the antenna is 2 or 3 times as wide as the vertex, the whole front opaque and pollinose, the ocellar tubercle unusually high and prominent, elongate, extending back behind the ocelli, and with the eye on each side rising above the base of the tubercle. The ocelli are placed in a short isosceles triangle. The antennae are separated by a distance equal the basal width of the antenna. Viewed anteriorly the large, oblique, subventral oral recess occupies the lower third of the head. It forms a wide, broadly oval, elongate recess with deep vertical walls, even anteriorly, and it is recessed backward at the base below. The proboscis is usually thrust directly forward or a little downward. Gena quite narrow but widening a little at the bottom of the eye and the tentorial fissure practically closed. From above the lobes of the occiput are separated by about half the width of the ocellar tubercle. The interior recess has an opaque membranous pillowlike extension arising from the cervix interiorly.

Thorax: The thorax is considerably longer than wide, much narrower than the head, rather opaque brownish or blackish, but with very dense, opaque, flat-appressed, somewhat flattened tomentum or pile that forms regular patterns directed in definite directions, mostly posteriorly but near the scutellum radiating outward, and anteriorly broken up into a more loose arrangement, semiappressed and nondirectional. Many species show distinct vittate strips upon the thorax. Pile of the scutellum quite similar to that of the mesonotum, the ground color, however, apt to be paler, especially apically. The humerus and postalar callosity are apt to be light in color, the humerus with humerus erect, long bristly hairs. The entire lateral margin back to the wing often has curled shining bristles. The noto-

pleuron with 2 or 3 quite long, stout bristles, 3 others above the wing, 3 or more upon the postalar callosity, 1 or 2 pairs in front of the scutellum, 3 pairs of especially long, curled, stout, pale bristles on the scutellar margin, weaker in some species, and with a dorsal central row of 6 or 7 bristles on the posterior part of the mesonotum. The mesonotum is rather strongly convex, the pronotum high, abrupt and vertical, upper mesopleuron with a band of loose upwardly directed bristles, and along its middle longitudinally, a band of matted, long, pale, scaliform pile. Whole pleuron generally pale and pale pollinose. The entire hypopleuron, metapleuron, metanotum, and pteropleuron, and all of the sternopleuron, except the upper border, without pile or bristles. The squama is almost bare. The plumula likewise, except for dense micropubescence. Halteres large, the stalk widened apically. The posterior spiracle is unusually large, oval, and widely open with a short pubescent fringe anteriorly, and there is a curious, flattened pit, posterodorsally next to the haltere.

Legs: Femora distinctly swollen on all three pairs, more stout than almost any bombyline except *Toxophora* Meigen. Anterior femur ventrally with a cluster of spines anteroventrally on the outer half as many as 8, and as many as 10 spinous bristles posteriorly. Middle femur with 10 spines posteroventrally. The hind femur with 4 or 5 short and 1 or 2 long spines anteroventrally, but with 4 or 5 quite long, quite stout spines or spinous bristles ventromedially and sometimes some shorter ones. Anterior tibia with numerous, short, oblique, spinous setae and short bristles anterodorsally, but with almost none elsewhere. Middle tibia somewhat similar, hind tibia, however, very long, stout, of uniform thickness with 4 groups of long, often white, stout bristles in pairs along the dorsal surface, and with an additional cluster at the apex. The tarsi are remarkably long and have a fringe of very stout, blunt spines along the ventral margin forming a comblike structure. These are on the anterior margin of the middle and hind tibia, and on the posterior margin the spines are somewhat longer and distinctly sharper. Austen (1937) called attention to the fact that several species of *Amictus* have one or more remarkably elongate bristles on the underside of the first segment of the front tarsus just before the tip. The claws in *Amictus* are unusually long, sharp, barely curved at the tip, and the long slender pulvilli extend almost to the apex of the claw.

Wings: Wing elongate and slender with wrinkled, iridescent surface. It may be totally hyaline or, as in species like *minor*, all of the crossveins may be diffusely margined with blackish brown. The furation of the third vein and anterior intercalary vein is blackish brown as well. The first posterior cell may be closed with a long stalk as in *validus* Loew, closed to the margin as in *tigrinus* Austen, or this cell may be open in maximal width as in *minor* Austen. In *variegatus* Meigen the first posterior cell is open, and there are 3 submarginal cells. The anal cell is always widely open, the

ambient vein quite stout and complete, the alula absent, the costa thickened at the base, but with minute setae and with a furry lappet in place of a hook.

Abdomen: Decumbent, distinctly compressed laterally so that the abdomen is nearly cylindrical, quite so on the second segment, and slightly more narrowed on the remaining segments. First segment as wide as the thorax with a conspicuous anterior brush of dense, pale, long, rigid, spikelike pile, which, however, is confined to the outer third of the segment, leaving none beneath the scutellum. The remainder of the first segment and all the remaining tergites are densely covered with a curious, flat-appressed mat of opaque or feebly shining, flattened pile or tomentum of different colors all so pale so that characteristic patterns are formed in different species. In addition, each tergite has on the posterior margin a single row of quite long, erect, conspicuous pale bristles, usually 5 on each side. The male terminalia are quite large and long, placed vertically and truncately at the end of the abdomen, the last segments increased in depth thereby, the dististyli exposed from above, symmetrical, directed backward, and the whole hypopygium laterally with a dense fringe of long, bristly hair.

The male terminalia from dorsal aspect, epandrium removed, show a pygidium that is wide basally, narrowing apically with a long slender ejaculatory process. In the lateral view, this process arises at the extreme base of the genitalia and curves downward and forward the full length of the genitalia and beyond. It is curiously suggestive of the condition found in *Paratoxophora* Engel, which also has this curious backwardly turned snakelike or tubelike ejaculatory process of extraordinary length, and the process also goes backward and turns downward and forward just as in *Amictus* Wiedemann. The two genera from their external morphology do not suggest a relationship, however, and there are significant differences in the genitalia as well. However, the basistylus of *Amictus* does not turn up proximally, and the epiphallus and dististyle are quite different, and the epandrium is also quite different. Numerous differences appear both from the dorsal and lateral aspect.

Material available for study: The species in this genus from both the National Museum of Natural History and the British Museum (Natural History). I also have material of *Amictus aegyptiacus* Paramonov received through the courtesy of the Department of Entomology of Cairo University in exchange for American bee flies.

Immature stages: Unknown.

Ecology and behavior of adults: Engel (1932) states that these flies are usually taken in April or May and again in autumn and are found in southern countries for the most part. They are taken from the flowers of steppe-loving plants.

Distribution: Neotropical: *Amictus cinerascens* Bigot, 1892.

Palearctic: *Amictus aegyptiacus* Paramonov, 1931; *castaneus* (Macquart), 1840 (as *Thlipsomyza*); *compressus* (Fabricius), 1805 (as *Bombylius*); *firuzianus* Paramonov, 1931; *funebris* Paramonov, 1931; *gebeli* Efflatoun, 1946; *heteropterus* (Macquart), 1840 (as *Thlipsomyza*); *insignis* Loew, 1870; *insularis* (Rondani), 1863 (as *Truguia*); *latifrons* Loew, 1873; *minor* Austen, 1937; *nobilis* Loew, 1870; *obliquenotatus* Austen, 1937; *oblongus* (Fabricius), 1805 (as *Bombylius*); *pictus* Loew, 1869; *pulchellus* Macquart, 1849 [= *striligatus* Loew, 1869]; *scutellaris* Loew, 1869; *setosus* Loew, 1869; *shafiki* Efflatoun, 1945; *similis* Paramonov, 1931; *tener* Becker, 1906; *tigrinus* Austen, 1937; *validus* Loew, 1869 [= *compressus* Wiedemann, 1828, without descr.]; *variatus* (Meig. in Walt's Reise), 1835 (as *Thlipsomyza*); *virgatus* Austen, 1937; *zinamominus* Becker, 1906.

Genus *Sinaia* Becker

FIGURES 212, 365, 604, 617, 638, 759, 973, 974, 975

Sinaia Becker, Ann. Mus. Nat. Hungarici, vol. 14, p. 65, 1916.
Type of genus: *Sinaia kneuckeri* Becker, 1916, by original designation.

Flies of medium size and of about the same size as *Amictus* Wiedemann to which it is closely related. It is readily separable by the much shorter face, which is gently rounded, the less attenuate antenna, shorter proboscis, and the characteristic shape of the male hypopygium, which I illustrate from Efflatoun. They are grayish black flies with a sheen of silvery pubescence or pollen not hiding the ground color. The proboscis is about as long as the head, and the bristles are even longer and stronger than in *Amictus* Wiedemann. Efflatoun (1945) notes that the statements of Engel with regard to *Sinaia* Becker are misleading because of the very bad preservation of the unique female type. He has been able to correct this because he had obtained a series of both males and females in perfect condition.

Sinaia Becker is known only from Sinai and from the Northern Sinai region; collected between April 13 and 24.

Length: 8 to 9.2 mm., breadth 10 to 12 mm.

Head: Head a little broader than the thorax; face feebly produced forward "beak-like"; proboscis as long as the length of the head; antennae as in *Amictus* Wiedemann, and the third segment bearing a minute cylindrical joint ending by a microscopic sensory rod.

Wings: Wings of the same shape and with the same venation as in *Amictus* Wiedemann and in the type of the genus, *kneuckeri* Becker, which is the only species known so far, cell R_2 is widely open and the r-m crossvein is placed well after the middle of 1st M_2 cell; 1st A cell open; alula obsolete.

Thorax: Thorax with weak but distinct rows of d.c. bristles; pre-alar, supra-alar and post-alar bristles well developed; scutellum with marginal bristles. Posterior femora with ventral rows of bristles and the tibiae with much fewer and shorter bristles except on the posterior tibiae where the short bristles are fairly numerous.

Abdomen: Abdomen with distinct marginal bristles particularly on the sides and toward the apex.

Material available for study: None. I have quoted Efflatoun's excellent and penetrating description, based upon a series of fresh individuals of both sexes; previously this genus has been only known from a single, much damaged female.

Immature stages: Unknown.

Ecology and behavior of adults: Not recorded.

Distribution: Sinai Desert (Ethiopian): *Sinaia aharonii* Engel, 1937; *kneuckeri* Becker, 1916.

Genus *Henica* Macquart

FIGURES 226, 406, 620, 973, 978, 1030

Enica Macquart, Hist. nat. Insectes. Dipt., Suite à Buffon, vol. 1, p. 399, 1834. Type of genus: *Anthrax longirostris* Wiedemann, 1819, p. 134, also 1828, p. 281, by monotypy.

Henica, emendation. See Kertész p. 69, 1909.

Lagochilus Loew, Öfvers. Kongl. Vet. Akad. Förhandl., vol. 17, p. 87, 1860. Type of genus: *Anthrax longirostris* Wiedemann, 1819, as *Cyllenina afra* Wiedemann, 1828, p. 358, by monotypy, not *Cyllenina afra* Macquart, 1840; see *Nomalonia*.

Alonipola Rondani, Arch. Zool. Anat. Fisiol., vol. 3, p. 71 (sep.), 1863. Type of genus: *Anthrax longirostris* Wiedemann, 1819, as *Cyllenina pluricellata* Macquart, 1855, by original designation.

We prefer *Henica* on basis of usage.

An odd fly, robust, of medium size, and brownish color with yellowish-white coloration on the head. The pile of the front, the sides of the thorax and scutellum and all tibiae and femora is decidedly bristly and its color black. The mesonotum and the whole abdomen, however, is covered with matted, appressed pile, slightly scaliform, of mixed colors, pale brown and brownish white or yellow.

The wings are quite distinctive; the costal cell is yellowish and the remainder of the wing brown, though paler on the posterior half; it has 8 distinct and conspicuous pale whitish fenestrate spots centered about the crossveins and vein furcations, and each of considerable size. There are 3 submarginal cells and the marginal cell is divided into 3 parts by 2 supernumerary crossveins. The second vein arises as a crossvein with backward spur. The wing is narrow basally, the alula narrow.

The occiput is bilobed and cuspulate but much more shallow than *Peringueyimyia* Bezzi and the lobes are separated. Its nearest allied genus is *Nomalonia* Rondani, which has a similar occiput and similarly has what Hesse describes as a muscoid appearance; *Nomalonia* Rondani differs principally in lacking the extra crossveins in the marginal cell; also the front and especially the sides of the face are bare in contrast to *Henica* Macquart which has not only a very bristly front but also has a conspicuous extension of pile down the side of each antenna.

Henica Macquart is a characteristic element of South African Diptera fauna, of which only one species is known.

Length: 4.5 to 11 mm., wing, 4.5 to 9.5 mm.

The exceptional confusion that has centered around *Henica* Macquart is because Wiedemann described a species as *Anthrax longirostris* Wiedemann, another as *Cyllenina longirostris* Wiedemann, and a third species as *Cyllenina afra* Wiedemann. The first two species were distinct, but placed in the wrong genera. It was later shown that his third species, *Cyllenina afra* Wiedemann, is really a strict synonym of his *Anthrax longirostris* for which Macquart erected the genus *Henica*, but not before additional genera had been proposed for it. Macquart, as a result of misidentification, also re-described *Anthrax longirostris* Wiedemann as *Cyllenina pluricellata* (1855). Rondani added to the confusion by creating a new genus *Alonipola* (1863) for it. Loew, realizing that Wiedemann's third species, *Cyllenina afra*, did not belong to this genus created the genus *Lagochilus* for it. *Lagochilus* Loew falls into synonymy under *Henica* Macquart.

Head, lateral aspect: The head is approximately hemicircular from lateral aspect, only a little produced in the middle at the attachment of the antennae. The occiput is only moderately produced but is slightly more extensive on the upper half, leaving the eye margins almost but not quite plane. The eye is circular in front but the entire eye forms less than half a circle. The pile of the occiput consists of a broad, wide band of scanty, fine, erect hairs on the wide posterior rim of the occiput. Pile is absent on the lateral margin of the occiput adjacent to the eye where only pollen is present, but on the inner margin of the occiput this scanty fringe is directed backward. The front is less convex than in *Nomalonia* Rondani, except along the eye margin it is covered with loosely scattered, rather long, stiff, black, slender bristles curved downward toward the antennae. Eye margins of the front with pollen.

The proboscis slender, about as long as in *Nomalonia* Rondani, generally held obliquely upward. The labellum may show a rugosity due to minute spinules in some lights. Palpus quite small and slender of no great length, with a few fine hairs near the apex, and composed of a single segment. The antennae are attached quite in the middle of the head; they are small and slender. The first segment is not quite as long as its apical width, a little narrowed at the base with a tuft of 6 or 8 setae ventrally, not extending to the end of the second segment; second segment cylindrical, as long as wide, with 3 or 4 black, dorsal setae at the apex. Third segment more slender, of about equal width to beyond the middle, beyond which it is reduced to about half the basal width. At the apex it ends in a small, oblique, medial, cup-shaped depression, bearing minute, enclosed spine.

Head, anterior aspect: The head as wide or wider than the thorax, the oragenal cup is less protrusive than in *Nomalonia* Rondani, but likewise reaches to the base of the antennae and is separated from the sides of the face by a deep, wide furrow, which on the lower fifth of the head merges into a long, quite deep, narrow, tentorial fissure. The front is large and triangular, the eyes

of the male separated by a space equal to the space between the posterior ocelli. All 3 of the ocelli are quite large and set in a short isosceles triangle. The ocellar tubercle is convex and raised and bears a tuft of numerous slender black bristles, those behind the ocelli erect, those in front curved forward. Front of the female much wider. The antennae are narrowly separated by a space equal to the width of the second antennal segment. The oragenal cup is quite deep below and although quite elongate is more shallow above with the inner wall sloping, both sides of the upper furrow covered with moderately dense, long, coarse pile curved downward. Pile is absent on the oral side of the tentorial fissure but abundantly present on the side opposite next to the eye. The genae, while extending downward below the eye, are not as extensive as in *Nomalonia Rondani*. From a vertical aspect, the two halves of the occiput do not meet above but leave a rather wide, deep sulcus or fissure behind the vertex.

Thorax: The thorax is moderately convex, more so than in *Nomalonia Rondani*, and the mesonotum is densely covered with appressed, coarse, narrowly scaliform pile, partly arranged in vittae of different colors. Very little of the black ground color shining through. Mesonotum anterolaterally and in front of the scutellum with some scattered, moderately long, fine, erect, bristly hairs. Sides of mesonotum, the scutellum, pre-scutellar area, and the pleuron pale, brownish-clay color, on the mesonotum and scutellum partly translucent. Humerus with pile and bristly hairs similar to that of the mesonotum. Notopleuron with a tuft of 7 long, sharp, curved, basally stout, black bristles. Four similar more slender bristles in a row above the wing; 3 or 4 longer ones on the postalar callosity and the scutellum with 5 pairs on the margin, besides a few other shorter, fine hairs. Greater basal part of the scutellum with appressed, pale, scaliform pile like that of the mesonotum.

Upper border of the mesopleuron with a conspicuous border of upwardly directed, rather numerous, black, bristly hairs. Metapleuron pollinose only. Metanotum likewise. Upper posterior hypopleuron behind the spiracle with a patch of appressed scales. Lower half of the pteropleuron with a large, dense patch of appressed scales directed forward. Entire ventral half of the mesopleuron densely covered with long, pale, flattened scales. Some similar scales on the sternopleuron. Squamae somewhat vesicular and with a fine fringe of marginal hairs. Haltere with the stalk dilated and flattened apically and bearing scaliform pile.

Legs: The legs are unusually stout, especially the femora. The anterior 4 femora are somewhat swollen toward the base. Hind femur stout. Anterior femur with a posteroventral row of 10 or 12 short bristles and 7 or 8 irregularly placed along the anterior surface. All coxae with 4 to 10 long, black, downwardly directed bristles. The whole surface otherwise covered with appressed, pale-colored scales. Middle femur similar to the anterior pair. Hind femur with a row of 8 or more

long, slender, downwardly directed black bristles on both anteroventral and ventromedial surfaces, and with a cluster of bristles dorsoapically in several rows. Anterior tibia with 9 prominent, black bristles posterodorsally and 5 or 6 shorter ones anterodorsally. Middle tibiae with 8 long, anterodorsal bristles and 12 or more fine, short posterior bristles, besides 5 long, stout, posteroventral bristles, and 8 anteroventral bristles. Hind femur with still longer bristles in 4 rows of 6 or 7 bristles each. All tibiae with 2 or 3 very long, stout, apical ventral bristles. Last 3 segments of tarsi in male with curious pads ventrally. Pulvilli minute. Claws short and rather stout.

Wings: The wings narrowed toward the base, largely brown villose except for large fenestrate, subquadrate spots with whitish villi on each side of all crossveins, 8 spots in each wing. Costal cell paler. There are 3 marginal cells and 3 submarginal cells. The second vein arises rectangularly simulating a crossvein or sometimes a double crossvein with backward spur. The rectangular anterior crossvein lies close to the outer fifth of the discal cell. The intercalary vein is long and straight. Anal cell very widely open. Axillary lobe narrow and the alulae quite narrow, ambient vein complete.

Abdomen: The abdomen is broad, wider than the thorax and only gently convex. Whole abdomen rather densely covered with narrow, appressed, mostly pale, scaliform pile with a little darker pile of a fine, bristly character forming borders along the posterior margin and the pale scales often of different colors. Ground color black.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium of male with the basal parts elongate, not separated into two parts by a dorsal suture, the line of suture being indicated only by a slight longitudinal depression towards apical part, with only very short and scattered fine hairs above and very fine pruinescence, but no long, bristly hairs; beaked apical joints, with the apical part more or less flattened and bifid, with a transverse, raised, keel-like ridge above, behind which the dorsum is covered with dense bristly hairs; aedeagus with the slender apical part curved upwards, then broad and tubular for some distance and then appearing very broad and really constituting part of the ventral inner part of basal part, the actual tube of the aedeagus being visible along its center; middle part of aedeagal complex prominent, inflated, helmet-like and, together with basal part of aedeagus, connected on each side by means of ramus to basal part and also to last sternite, with the ramus on each side continued on inner side of basally directed projection of basal part as a narrow, strap-like process; lateral struts shortish.

Material available for study: Through the courtesy of Dr. A. J. Hesse I have been able to study a pair of the type-species. The British Museum (Natural History) also gave me a specimen of that species.

Immature stages: Unknown.

Ecology and behavior of adults: I have no record of habits and behavior or flower preferences of the adults.

Distribution: Ethiopian: *Henica longirostris* (Wiedemann), 1819, 1828 (as *Anthrax*) [= *afra* (Wiedemann), 1828 (as *Cyllenia*), = *puricellata* (Macquart), 1855 (as

Cyllenina), also=*pluricellata* (Macquart in Rondani), 1863 (as *Alonipola*), also=*afer* (Wiedemann in Loew), 1860 (as *Lagochilus*)].

Genus *Nomalonia* Rondani

FIGURES 224, 225, 363, 609, 612, 696, 728, 994, 995, 996

Nomalonia Rondani, Arch. Zool. Anat. Fisiol., vol. 3, p. 71, 1863.

Type of genus: *Cyllenina afra* Macquart, 1840, not Wiedemann, by original designation.

[*Nomalonia* Rondani, like *Henica* Macquart, has suffered from a confusion due to two species with great superficial similarity—which in early collections were rarely seen—and were poorly understood. Macquart (1840) described a species as *Cyllenina afra* Wiedemann, which proved to be not that species, but an undescribed species which Rondani later made the type of a new genus, *Nomalonia afra* Macquart.]

Hesse (1956), pp. 34-36, key to 6 Ethiopian species.

Brownish flies with appressed pile on abdomen and mesonotum. Closely related to *Henica* Macquart in general form, coloration, and prominence of the black bristles on the sides of thorax, on the scutellum, and the legs. It is distinguished primarily by the absence of the additional crossveins in the marginal cell and the wing is less conspicuously infuscated and fenestrate. The sides of the face opposite each antenna and the face itself below the antenna are quite bare, rather polished and shining in contrast to the dense subappressed pile that is present in *Henica* Macquart.

Nomalonia is a South African genus with at least 6 species.

Length: 6.5 to 12 mm.; of wing 6 to 10 mm.

Head, lateral aspect: The head is more or less triangular in profile, more especially in the male. In both male and female the front is convex, swollen, and somewhat protuberant, but in the male the margin of the oragenal cup appears to be more plane. The occiput is only moderately developed, far less extensive than in *Peringueyimyia* Bigot. It is almost equally long above and below and the posterior margin of the eye is almost but not quite plane. From near the top to shortly above the lower corner there is an almost imperceptible curve or excavation. Pile of the occiput very short and scanty, almost nonexistent close to the eye but becoming longer and forming a distinct fringe backward, of no great length along the inner margin of the occipital cup. The halves of the occiput do not meet above behind the vertex and leave a rather wide gap between the occiput almost equal to the space between the posterior ocelli. The front in the male is pale waxy yellow as is the entire head, except the inner rim of the occiput. It is rather strongly swollen and a little convex from the lateral aspect and bears scattered, bristly black hairs down the middle, and in addition upon a triangular area above the antennae there is abundant, long, subappressed, white scales. These scales extend more scantily to the ocelli. The ocellar tubercle is swollen and conspicuous. The ocelli are large, especially the poste-

rior ones. In the female there are rather more black bristles than yellowish scales on the front.

The proboscis is elongate and quite slender, about $1\frac{1}{2}$ times as long as the head but the part that extends beyond the buccal cavity is no longer than the head; it tends to be held obliquely upward and outward. The palpus is long and quite slender and composed of one segment only; it is much more slender than in *Peringueyimyia* Bigot. It is deeply recessed, composed of a single segment and colored so like the background of the cavity that it is not easily perceived. The antennae are relatively small but slender, except the first segment, which is a little swollen, very short, distinctly beadlike and pale yellow. The second segment is no longer, but is cylindrical, scarcely more than half as wide as the first segment, and the third segment is a little more narrow at the base and attenuate on the outer two-thirds, with a short, stublike, apical microsegment. Whole apex of the third antennal segment colored black. The first antennal segment has only a few minute setae below, the second segment has a few setae above at the apex, and the third segment has 3 or 4 setae dorsally. The third antennal segment is twice as long as the first two segments combined.

Head, anterior aspect: Viewed from in front the head is narrowly oval with the genae swollen and prominently extended down beneath the eyes. The head is as wide as the thorax. The eyes in the male are separated by a space equal the width of the first antennal segment. There is a distinct sulcus separating the face from the front and continuing laterally in the direction of the eye and ending in a deep tentorial pit, and then continued obliquely downward separating the genae from the sides of the oragenal cup. In the female the front is quite wide both above as well as below. The ocelli occupy a triangle not quite equilateral and are separated from the eye on each side by a distance equal to the width of this triangle. The antennae separated by a space equal to the length of the second antennal segment. The oral opening is large, wide, elongate, and quite deep. It extends to within a short distance of the antennae forming a somewhat nose-shaped or peaked extension beneath the antennae, so that the midfacial area below the antennae is quite short. Sides of the oragenal cup and face with pollen only and shining waxy yellow. It is therefore in great contrast with *Peringueyimyia* Bigot. There tends to be a brownish spot on each side near the bottom of the eye.

Thorax: The mesonotum is rather short and moderately convex, especially on the anterior half. The pile is composed of comparatively dense, appressed, brownish-yellow scales, usually more or less denuded over the middle of the mesonotum, and more abundant on the anterior lateral margins and in front of the scutellum and on the base and sides of the latter. Middle of the mesonotum broadly polished black bearing pollinose vittae when viewed from the front. There is a scanty, anterior fringe of pile around the borders of the extremely short prothorax. The humerus is prominent,

and somewhat swollen; it bears pale scales and a few black bristles. Notopleuron with a double row of strong, black bristles, 4 above and 3 much stouter and longer below. Above the wing there are 3 slender black bristles, and there are 5 long, stout, curved black bristles in a single row on the postalar callosity. Postmargin of the scutellum with 4 curved black bristles, not quite as long as those of the postalar callosity. The humerus, lateral margins of the mesonotum, prescutellar area and the whole of the scutellum are light yellowish brown. This yellow area in front of the scutellum is bisected with black. Metapleuron and sides of the metanotum without pile; hypopleuron and pteropleuron likewise bare. The mesopleuron on the upper border has a wide longitudinal row of stout, black, upturned bristles. The lower part of mesopleuron has a few scattered, pale, brownish yellow, lanceolate scales similar to those of the mesonotum. There is a small patch of similar scales in the middle of the sternopleuron.

Legs: All coxae have a vertical row of stout, black bristles, the legs are stout but comparatively short, the anterior femur is a little swollen toward the base and bears a few black bristles below in the middle and posteriorly. Middle femur with 3 or 4 black bristles ventrally, and with appressed, linear, black scales above and shorter, broader, pale scales below. Hind femur stout and rather thick throughout with 6 stout, black, anteroventral bristles; there are 3 others at the apex laterally and 2 above, and with the scales abundant and almost entirely pale. The anterior tibia has irregular, dorsal rows of stout, spiculate, black bristles, 8 or 10 in each row, and 7 or 8 posteriorly. The apex of this tibia has 4 long, stout, sharp, black bristles. The 2 ventral bristles are more prominent. Middle tibiae with similar apex, the hind tibia with a circlet of 8 or 9 stout bristles, and with 6 long, anterodorsal bristles, 4 or 5 shorter anteroventral bristles and 9 long, stout, posterior bristles. Tarsi rather short, the pulvilli greatly reduced, the claws almost straight, only slightly curved toward the apex.

Wings: The wings are rather conspicuously brown villose and subhyaline with whitish, opaque, conspicuous spots on the crossveins, apex of the second basal cell and base of third vein. There are 3 submarginal cells and the base of the anterior branch of the third vein arises steeply and plane and obliquely, simulating a crossvein. The second vein arises abruptly and rectangularly and often has a distinct spur vein directed backward. The significance of this spur is uncertain. The first posterior cell is widely open, the rectangular, anterior crossvein is near the outer fifth of the discal cell, the lower marginal vein of the discal cell is straight except at the base where it is curved. Anal cell very widely opened, ambient vein complete, alula rather narrow. Base of costa a little swollen, the scales and fine setae and a triangular lappet present instead of a costal hook. The first vein ends no great distance from the end of the second vein. Marginal cell narrow at the apex.

Abdomen: The first and second segments of the abdomen in the male are as wide as the mesonotum and the first four segments in the female are as wide or even wider than the thorax. The abdomen is very slightly convex, moderately narrowed and compressed laterally in the male. The color tends to be more or less shining black, on the basal parts of the tergites becoming diffusely reddish brown along the posterior margin and sometimes over most of the posterior tergites. The pile consists of flat-appressed, black setae, rather densely mixed with appressed, reddish brown, short, wide scales that become brownish white along the posterior margins especially toward the sides of the tergites. On the posterior tergites toward the sides of the setae give way to longer, slender, flat-appressed, bristly hairs. Male terminalia elongate, large, and prominently protruded. Hesse (1956) points out that the basal portion of the hypopygium, like that of *Henica* Macquart, is fused dorsally and ending basally on each side in a lobelike prolongation. The dististyli are excavated or hollowed on the sides below and the inner excavation is often produced apically into a toothlike lobe.

Because of the large number of species that Dr. A. J. Hesse was able to study and summarize, I quote his work on the hypopygium of the males:

Hypopygium of the male is also very similar to that of *Henica* in some respects; basal parts also fused dorsally, elongate, ending basally on each side in a lobe-like prolongation; beaked apical joints excavated or hollowed on the sides towards the lower aspect, the inner excavation often produced apically into a tooth-like or prong-like lobe which gives the joints a bifid appearance from above, dorsally these joints are covered with shortish, sometimes spine-like, bristles; apical joints usually also end in a sharp point, but they may be blunt and, when viewed from above, their shapes are variable; aedeagus tubular as in *Henica* and also constitutes part of ventral aspect of basal parts, being fused ventrally with the basal part; middle part of aedeagal complex helmet-shaped and intimately connected with the last sternite by membranous or chitinous connection; lateral struts usually broadish, ladle-shaped, ovoid or tongue-shaped; basal strut racket-shaped or chopper-shaped.

Material available for study: I have a pair of the type-species most kindly sent by Dr. Hesse for study and dissection.

Immature stage: Unknown.

Ecology and behavior of adults: I have seen no published record of the behavior of the adults, or its preference for flowers.

Distribution: Ethiopian: *Nomatonina afra* Macquart, 1840 [= *Cyllenia afra* Wiedemann, in Marquart, misid.]; *clavicornis*, Hesse, 1956; *henicoides* Hesse, 1956; *imitata* Hesse, 1956; *sporangthera* Hesse, 1956; *syrticola* Hesse, 1956.

Genus *Tomomyza* Wiedemann

FIGURES 113, 115, 362, 603, 613, 1021, 1022, 1023

Tomomyza Wiedemann, Nova Dipteronum Genera, p. 9, 1820a.

Type of genus: *Tomomyza anthracoides* Wiedemann, 1820, by monotypy.

Hesse (1956), pp. 74-77, key to 11 Ethiopian species.

Small flies of relatively bare aspect due to dense, minute, appressed pile. They are only moderately elongate; the abdomen is cylindrical and long ovoid, rather than elongate, in the same extent as in *Paracosmus* Osten Sacken. *Tomomyza* Wiedemann is more like *Pantostomus* Bezzi, from which it differs in the generally mottled wings and the erratic venation in the submarginal part of the radial field. The hind femur tends to be somewhat thickened distally and lacks bristles or spines; the face and front are long conical or triangular and the proboscis does not extend beyond the oral recess; lobes of occiput tightly apposed.

Tomomyza is a small genus of South African flies.

Length: 4 to 11 mm., usually about 5 to 8 mm.; wing, 3.5 to 8 mm.

Head, lateral aspect: The head is subglobular though with strongly peaked and forward production of face and front at the middle of the head. The occipital component is unusually prominent, especially above, but also at the bottom of the head; it is least extensive near the lower sixth. The posterior occiput laterally is rather steeply sloping, a little convex, so that the interior cup or recess is quite large, circular and deep. The pile of the occiput is dense, minute, and appressed, extending all the way to the eye margin and the inner margin of the occiput has a fine, erect, sparse fringe. The front and face are quite prominent as a result of their peaked forward extension. The oragenal cup, which reaches quite to the antennae is even more extensive, extending beyond the first antennal segment. The front is plane across the eye on the upper half, well developed below and bears considerable, fine, moderately long, subappressed pile running from the whole of the vertex widely down the middle of the front to the base of the antennae. The whole of the front and all the vertex is densely micropubescent, except the low ocellar tubercle, which is nodular behind and, except for a medial stripe on the upper half of the front and vertex, and except a small spot along the eyes in the middle of the front, the sides of the frontofacial area opposite the antennae are flat and covered only with dense, silvery micropubescent. Similar pubescence continued on down the sides of the face to a point just below the middle of the eyes. The oragenal cup is largely bare, and shining, separated from the face by a very shallow, oblique depression. The eye is large, occupying the greater part of the head; the posterior margin is nearly plane. The upper anterior facets are somewhat enlarged.

The proboscis is short and rather stout, laterally compressed, the labellum is elongate but narrow, curved upward and attenuate to the apex. The palpus is quite long and slender, curved, with short, apical, clublike segment. The long, curved basal portion has a few long, scattered, ventral hairs. The antennae are attached at the middle of the head; the first segment is stout but not swollen, widened apically, longest medially, and this segment is less than twice as long as its basal width. The second segment is short and beadlike,

rather longer medially, so that the flattened pyriform third segment which is shaped much as in *Pantostomus* Bezzi is held strongly outward. The first two segments bear only dense, minute, appressed pubescence. The third segment is pollinose and bears a minute, apical spine.

Head, anterior aspect: The head is circular and distinctly wider than the thorax. The eyes in the male are separated in both sexes, narrowly in the male, more widely in the female, the extent variable, but generally about 3 times the width of the ocellar tubercle, but in some instances twice the width of the ocellar tubercle. The antennae are widely separated by a strong, triangular production of the front similar to *Pantostomus* Bezzi, yet the first two segments lie adjacent at the apex. The ocellar tubercle is short isosceles and situated a short distance forward from the posterior eye corners. The oragenal cup is deep and long and narrow, extending quite to the base of the antennae from the bottom of the eye. Its inner wall is vertical, the middle portion of the outer wall is obliquely sloping but steep. Genae reduced to a mere line of pubescence, and similarly reduced at the bottom of the head. Tentorial fissure absent. From vertical aspect the occiput is bilobed and has a dorsal fissure. It has a conspicuous sunken depression where the occipital lobes meet the posterior vertex; they meet at a point still some distance behind the eye margin. Sides of occipital lobes touching.

Thorax: the thorax is slightly convex, the mesonotum generally opaque blackish with paler borders laterally. The humerus and scutellum are more or less pale. Pile of mesonotum dense, fine, curled, and flat-appressed giving way to slightly longer, coarse hairs directed outward along the lower margin of the notopleuron and tufts of erect, slightly flattened hairs on the humerus. The pile of the scutellum is similar to the mesonotum; the curled hairs of the margin are a little longer. Metapleuron pilose, hypopleuron with micropubescent only, pteropleuron without pile. The pile of the mesopleuron on the upper part consists of only appressed micropubescent.

Legs: The legs are relatively short, the anterior 4 femora are slender, the posterior pair distinctly swollen a little toward the apex. The pile of the femora and tibiae is minute, rather dense, and quite flat-appressed, pale and glittering at least in part on the tibiae. Hind tibia and femur sometimes banded, due to darker pile apically. Pulvilli slender and linear, as long as the claw. Claws very fine, sharp, and slightly curved at the apex.

Wings: The wings have erratic venation with numerous dark, brownish spots on the crossvein, the whole of the first basal cell, except near the apex, the whole of the costal cell and basal half of the marginal cell. There are 3 submarginal cells. The first submarginal cell is indented on each side by a rectangular apex to the marginal cell and by a rectangular bend in the last section of the anterior branch of the third vein. This

section of the third vein also arises as a crossvein placed rectangularly and connects with the second vein by a rectangularly bent vein, which often emits a spur basalward. Other bends in veins above described often emit spurs. Hesse (1956) figures one species with a venation very little different from that of *Paracosmus* Osten Sacken. The numerous crossveins and right angle bends are absent. First posterior cell open but narrowed, lower vein of the discal cell with one or more spurs at bends and the anterior crossvein lies well beyond the middle of the discal cell. Anal cell open, ambient vein complete, ahula absent.

Abdomen: The abdomen is moderately elongate, the tergites rather strongly convex from side to side. Seven tergites are present; the pile is short, dense, fine, not flattened and quite flat-appressed. On the sides of the first segment the pile is slightly longer and directed outward and appressed. Female terminalia concealed within compressed seventh tergite and border of short pubescence. Hesse (1956) points out that the last sternite in the male is dorsal in position, the basal part composed of a single, undivided part generally covered with dense hairs, ending on each side basally with a lobelike process. The dististyli form a more or less curved clawlike structure. Aedeagus as in *Pantostomus* Bezzi but apex sometimes much recurved.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium of male also situated on the ventral aspect of abdomen as in *Pantostomus*, the last sternite of which is dorsal in position; basal part of hypopygium also composed of a single and undivided part, usually covered with fairly dense hair, ending basally on each side in a sort of process or lobe and in two known species at least also with an outwardly projecting process at base of this lobe, with the outer apical angle of basal part usually slightly produced and rounded; beaked apical joints usually curved claw-shaped; aedeagus shaped much as in *Pantostomus*, but sometimes with the apex much recurved.

Material available for study: Four species available through the generosity of Dr. A. J. Hesse of the South African Museum, Capetown.

Immature stages: Unknown.

Ecology and behavior of adults: Hesse (1956) records species of *Tomomyza* Wiedemann captured on flowers of *Carpobrotus edulis* and *Carpobrotus acinaciformis* and also resting on the sand between such plants. Another species of this genus was found resting or flying among branches and dried twigs of *Mesembryanthemum*. Still a third species was found resting on bare stones or ground or sand between bushes. A fourth species was caught on the sandy banks of a dry river course and also of the flowers of *Mesembryanthemum*.

Distribution: Ethiopian: *Tomomyza anomala* Hesse, 1956; *anthracoides* Wiedemann, 1820; *barbatula* Bezzi, 1922; *guillarmodi* Hesse, 1956; *karooana* Hesse, 1956; *nitidula* Hesse, 1956; *pallipes* Bezzi, 1922; *pantostomoides* Hesse, 1956; *philoxera* Hesse, 1956; *pictipennis* Bezzi, 1921; *stenolopha* Hesse, 1956.

Genus *Pantostomus* Bezzi

FIGURES 111, 356, 602, 614

Pantostomus Bezzi, Ann. South African Mus., vol. 18, p. 474, 1921b. Type of genus: *Pantostomus gibbiventris* Bezzi, 1921b, by monotypy. This is the first mention of this genus. Also Broteria (Ser. Zool.), vol. 20, fasc. 2, pp. 69, 79, 1922a.

Hesse (1956), pp. 53-55, key to 9 Ethiopian species.

Small flies with slightly elongated abdomen and with a very bare aspect due to the presence of appressed, scaliform pile. Closely related to *Paracosmus* Coquillett, and with similar venation, it differs in the presence of a very long, high, ocellar mound or tubercle. The ocelli are set almost halfway between front and posterior eye corners. Also, in *Pantostomus* Bezzi the lateral frontofacial area forms a strong, rugose, pillow-like support on each side of the antenna, and there is a deep foveal groove or sulcus setting off the upper rim of the genofacial cup or buccal cavity.

In *Pantostomus* Bezzi species that I have seen, the abdomen is strongly bulbose on the dorsal tergites and corrugate when seen from the sides, much in contrast to *Paracosmus* Coquillett.

This genus is also related to *Tomomyza* Wiedemann; that genus differs in having the wings generally mottled with brown spots and the venation, especially in the anterior apex or submarginal area, much more erratic. In *Pantostomus* Bezzi the wings are generally glassy hyaline but sometimes tinged with pale brown or yellow.

Pantostomus Bezzi is a South African genus which is a characteristic element of that fauna; Hesse in his remarkable work on this bee fly fauna has added 8 new species to the one partially described by Bezzi.

Length: 5 to 10 mm.; wing, 3.5 to 7.5 mm.

Head, lateral aspect: Head more or less triangular from the lateral view; the occiput is rather strongly developed on the upper half of the head, a little less so below. The central interior of the occiput is very widely and deeply cuplike and deeply recessed. The occipital pile is distinctly sparse and consists mostly of scattered, slender, scaliform hairs quite appressed and directed outwardly toward the eye margin. Along the inner rim of the occiput there are only a few, quite short, fine erect hairs. The front is plane across the eyes for only a very short distance at a point about one-third of the distance from the antennae to the posterior eye corners. The posterior parts of the front and the vertex are a little swollen, and the unusually long ocellar triangle long isosceles and set anteriorly a considerable distance from the eye corners. The lower third of the front, like the face, is prominently extended forward and on each side, adjacent to the antennae, there is a somewhat pillowlike, convex, transversely striate, moundlike swelling. The pile of the front consists of sparse, curled, flat-appressed, shining scales and on the ocellar tubercle there is some short, stiff, pale hairs curled forward in a medial row. The

oragenal cup extends obliquely upward and forward to the base of the antennae, at which point it extends forward nearly the length of the first antennal segment and is laterally separated from the face by a rather deep sulcus or crease. The eye is quite large, occupying by far the greater part of the head. The anterodorsal facets are very little enlarged, the whole anterior contour is hemicircular. The posterior margin is shallowly concave about the middle.

The proboscis is short, and relatively stout; the labellum is elongate and strongly tapered from the base to the rather sharp apex. The outer margin straight, the inner margin curved. Its length is a little less than that of the head. The palpus is quite long and slender. It is often curved and the apex is rather abruptly and slightly enlarged and swollen forming a very short terminal segment. The lateral margin has some fine, long, erect hairs, the remaining portion with minute, short hairs. The antennae are situated at the middle of the head; the first segment is short, ranging from barely longer than the second to slightly more than twice as long. It is more or less cylindrical, narrow at the base, a little widened at the apex, and bearing minute, appressed hairs. The second segment is quite short, slightly widened apically, and similarly pilose. The third segment is basally nearly twice as wide in some species; in others scarcely wider. It gradually narrows toward the apex leaving the whole segment long or short pyriform, thus rounded at the base though broad and narrowed apically. Dorsally at the apex it bears a minute, upturned spine.

Head, anterior aspect: The head is considerably wider than the thorax, the eyes separated in the male by a distance fully equal to the width of the antennae at the base. In the female the eyes are separated by only about twice the distance between outer margins of the posterior pair of the ocelli. The antennae are rather widely separated at the base, although this is not immediately apparent since they often touch one another. There is a strong, triangular extension of the front produced between the bases of the antennae. The oragenal cup is quite long, extending from the bottom of the eye to the base of the antennae. It is also deep, both inner and outer walls steep and vertical. The gena is reduced to a linear strip, except at the bottom of the eye, and the tentorial fissure is absent. From a dorsal aspect the occiput is bilobed, the halves touching.

Thorax: The thorax is gently convex, the mesonotum covered with dense, very short, curled appressed and flattened pile which becomes longer and still appressed along the lateral margins. The metapleuron has a large tuft of long, coarse, flattened, appressed shining pile. Posterior hypopleuron with a patch of flattened pile behind the haltere, and the anterior hypopleuron with a similar patch of appressed pile. The pteropleuron is shining and bare, except for a small, posteroventral patch of micropubescence; upper sternopleuron with similar micropubescence; upper border of the meso-

pleuron with scattered, sparse, appressed, flattened hairs.

Legs: The legs are rather short, the anterior 4 femora rather slender, the hind femur stout and a little swollen through the middle and beyond. Femora and tibiae with sparse, flat-appressed, glittering, scaliform pile. Pulvilli large, nearly as long as the claw, broad apically, the claws long and sharp, curved at the apex.

Wings: The wings are hyaline; 2 submarginal cells are present; the anterior branch of the third vein arises rectangularly at the crossvein and has a backward spur. Marginal cell rather strongly swollen and bulbous at the apex. First posterior cell slightly narrowed on the margin. Anal cell widely open; alula absent, ambient vein complete.

Abdomen: The abdomen is comparatively robust, moderately elongate, somewhat drooping; the first segment is short, shorter than in *Paracosmus* Osten Sacken. The second, third, and fourth segments have a wide but rather strongly raised, bulbose ridge down the middle with a strong depression on each side and an outlying bulla. Pile rather dense but short, flat-appressed, glittering, and scaliform. I find 5 long tergites and 2 very short ones. The male terminalia are strongly recessed within the abdomen in contrast to *Paracosmus* Osten Sacken. Hesse (1956) points out that the last sternite is dorsal in position; the basal part is undivided but covered with fine, dense hairs. The dististyli are claw-shaped from lateral aspect and much flattened or laterally compressed. Apical part of aedeagus curved upward a little; basal strut in some species with a distinctly visible lateral process on each side basally. He notes that the hypopygium of male is very uniform and similar in all the species.

Material available for study: A pair of the type-species kindly furnished by Dr. A. J. Hesse, and a paratype of *capensis* Hesse presented to me by the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Hesse (1956) comments on the habits of these flies. One species frequents sandy patches between shrubs. Still another species was caught resting on sand, and a third species was found on the dried twigs of *Mesembryanthemum*; when resting, their wings lie beside the abdomen and their reddish color harmonizes with the twigs and foliage of this plant.

Distribution: Ethiopian: *Pantostomus bullulatus* Hesse, 1956; *capensis* Hesse, 1956; *fruticicolus* Hesse, 1956; *gibbiventris* Bezzi, 1922; *mallochi* Hesse, 1956; *melanotidus* Hesse, 1956; *pilosulus* Hesse, 1956; *psamophilus* Hesse, 1956; *tinctellipennis* Hesse, 1956.

Genus *Amphicosmus* Coquillett

FIGURES 110, 114, 361, 608, 618

Amphicosmus Coquillett, West American Scientist, vol. 7, p. 219, 1891b. Type of genus: *Amphicosmus elegans* Coquillett, 1891b, by monotypy.

Glycophorba, new subgenus. Type of subgenus: *Amphicosmus cincturus* Williston, 1901.

Hall (1957), p. 142, key to 3 species.

Small slender, shining flies of bare or denuded aspect due to the minute pile. The glassy, hyaline wing has 3 submarginal cells and the end of the marginal cell is simple, not bulbous or swollen as in *Paracosmus* Osten Sacken; consequently *Amphicosmus* Coquillett is more closely related to *Metacosmus* Coquillett and like it has weak legs and the female front is convex, never concave.

There appears to be some sexual dimorphism; I took what I consider to be a pair at the same spot in Arizona; the female has the lower front, lower face, and lower occiput, besides tibiae, bright canary yellow; the male has these parts black or steel gray, the tibiae brown.

Amphicosmus Coquillett is a Nearctic genus known from arid western lands.

Length: 7 to 9 mm.

Head, lateral aspect: The head is globular, the occiput is moderately prominent, a little more so above. Viewed from the rear the occipital margins are wide and rather strongly convex and sloping to the eye margin and covered with dense, short, micropubescence and some pollen, the ground color shining through. The inner margin of the deep, interior cup has a very fine fringe of short, scanty hairs directed backward. The face is conically or triangularly produced forward much as in *Metacosmus* Coquillett. The pile of the face consists of a curious, oval downward extension of the dense micropubescence of the front; this reaches to the anterior margin of the oragenal cup well below the polished, bare upper part of the triangular face and extends obliquely forward beneath the antennae. Margin of the oragenal cup with a few minute hairs. The front is plane with the eye on the upper half, but visible in profile on the lower third at least where it extends forward a space equal to the length of the first two antennal segments. Its pile is moderately abundant, fine and suberect. The vertex and the very low ocellar triangle have equally fine, scanty hairs. The eye is quite large, although proportionately smaller than in *Metacosmus* Coquillett; the posterior margin is almost but not quite plane, and the oragenal cup extends in lateral aspect distinctly beyond the eye margin. The proboscis is short, but is nearly as long as the eye and is extended straight forward with comparatively slender though apically attenuate, flattened, divergent labellae that are curved on both inner and outer margins. The palpus is minute and slender, elongate, lying laterally along the sides of the proboscis, with 1 or 2 apical hairs.

The antennae are small, the first segment and the second subequal, shorter than high, pollinose, with 3 or 4 minute short, pale hairs apically both above and below. Third segment long conical in the male, a little longer than the first two segments combined and with minute apical spines. In the female it is a little more

widened through the middle and more abruptly narrowed toward the apex. The antennae are attached a little above the middle of the head.

Head, anterior aspect: The head is circular, the genae and oral opening very slightly produced below in the female, but scarcely at all in the male. The ocellar tubercle is also more prominent in the female. In the male the eyes are divided or separated by a space equal to the width of the third antennal segment. The ocelli occupy a long isosceles triangle and are set a considerable distance forward in front of the posterior eye corners, but are much closer to the posterior eye corners than in *Metacosmus* Coquillett. The female front is 3 or 4 times as wide as the front in the male, and the antennae are quite narrowly separated. Orogenal recess elongate, rather narrow, quite deep with steep vertical sides medially, and the vertical wall also steep laterally. There is a small, tentorial pit, rather shallow, at the eye margin about halfway up along the middle of the oral cup. Genae completely occluded by the development of the eye margin, except near the bottom of the eye where it is possible that the lower vertical wall of the oragenal recess, where it protrudes below the eye, is probably part of the genae. From the dorsal aspect the occiput is bilobed with a very narrow, linear fissure visible behind the vertex, the sides of the occiput appear to be almost or quite touching.

Thorax: The thorax is gently convex, the mesonotum polished black with rather sparse, fine, erect pile, and some pollen on the notopleuron. Humeri rather lobate with strong recess immediately behind and with a flared, liplike outer rim, which is pollinose, that separates mesonotum and mesopleuron. The upper border of the mesopleuron is also pollinose. Pleuron polished black, except sometimes the upper border of the mesopleuron, anterior metapleuron, the humerus, a notopleural spot, and the upper border of the postalar callosity, all of which are pale, polished yellow. Scutellum polished black with much erect, rather long fine hairs. Metapleuron with a dense tuft of long, bushy, often pale, coarse, flattened hairs; its surface is pollinose only. Metanotum shining and bare; hypopleuron with coarse micropubescence. Pteropleuron without pile, and the sternopleuron dorsally with a patch of appressed setae. Haltere with a very large club at the apex.

Legs: The legs are rather short, especially the femora which are moderately stout but not swollen. Both femora and tibiae without bristles, covered rather densely with short, appressed, shining, sharp, somewhat flattened or scaliform hairs that become longer on the hind femur. Pulvilli large, as long as the claw. Claws strongly curved at the apex.

Wings: The wings are hyaline, glassy, with 3 submarginal cells. First posterior cell widely open, the anterior crossvein lies a little beyond the middle of the discal cell. The anal cell is widely open, the ambient vein complete, the alula quite narrow.

Abdomen: The abdomen is elongate, slender, and laterally compressed. It is largely shining in color, generally light reddish brown, black on the first segment, except for a pale yellow, posterolateral spot, and black at the base of the second segment and on the terminal segments. Female terminalia enclosed by a fringe of large, flattened hairs arising from the inner surface of the last tergite. The male hypopygium as in *Paracosmus* Osten Sacken is large, strongly protruded, and the basimeres and dististyli are turned upward and flared outward, sharp, curved, and hooklike.

Material available for study: Representatives of the type-species at various museums and also a pair collected by the author in the western part of Arizona.

Immature stages: Unknown.

Ecology and behavior of adults: I have found this species resting upon hot, desert-crusted soil among weeds and herbs in lower Arizona in August; this habit is very similar to that of *Paracosmus* Osten Sacken.

Distribution: Nearctic: *Amphicosmus arizonensis* Johnson and Johnson, 1960; *cincturus* Williston, 1901; *elegans* Coquillett, 1891; *vanduzeei* Cole, 1923.

Glycophorba, new subgenus

Type of subgenus: *Amphicosmus cincturus* Williston, 1901.

Flies with club-shaped abdomen, a conical face that extends well beyond the end of the second antennal segment, and which have the wing containing 3 submarginal cells as in *Amphicosmus* Coquillett. They are related to *Amphicosmus* Coquillett and differ in the much larger size, the noncompressed, club-shaped abdomen, and in the venation. The anterior branch of the third vein arises in a long, rounded arch, and the marginal cell is much more widely swollen. Also, the lower surface of the hind femur is densely covered with rather long, dense, oblique stiffened hairs. The dense patches of microspinules present on the sides of the tergites in *Amphicosmus* Coquillett are much more poorly developed.

Flies from central Mexico.

Length: 14 mm.; of wing 10.5 mm.

Genus *Metacosmus* Coquillett

FIGURES 118, 355, 615

Metacosmus Coquillett, West American Sci., vol. 7, p. 220, 1891b.

Type of genus: *Metacosmus crilis* Coquillett, 1891, by monotypy.

Melander (1950b), p. 156, key to 3 species. All Nearctic.

Small, slender, shining black flies of bare aspect, with the abdomen rather elongate, especially in males, and often somewhat compressed. The postmargins of the tergites are linearly yellow or whitish. The head in *Metacosmus* Coquillett is larger than the entire thorax and wider. The ocelli are set far forward, the anterior

ocellus almost midway between antenna and occiput. There are 2 submarginal cells and 4 posterior cells. The anal cell is as widely open on the wing margin as the first posterior cell; axillary lobe present and whole wing glassy hyaline. The genus is more closely related to *Amphicosmus* Coquillett than to *Paracosmus* Coquillett; in the latter genus the female front is concave and the hind legs more stout; in *Metacosmus* Coquillett the legs are weak and the front convex; also the marginal cell is swollen, or bulbous at the apex in *Paracosmus* Coquillett and the anterior branch of the third vein arises as a simulated crossvein, with backward spur. This vein arises simply and obliquely without a spur in *Metacosmus* Coquillett. All three genera have the males dichoptic.

Metacosmus Coquillett is a Nearctic genus. One species is known from Pennsylvania, and I have taken it in New Jersey; the other two species are desert frequenters and known from Arizona, New Mexico, and California.

Length: 4 to 5 mm.

Head, lateral aspect: The head is nearly globular and quite elongate; the eye is enormously developed and constitutes the major part of the head. Its anterodorsal facets are much enlarged. The entire head is larger than the thorax, much wider and equally long. The occiput is rather strongly developed on the dorsal half of the head, viewed from the rear it is wide but it only gradually and gently slopes down to the eye margin. The interior cup is quite deep and abruptly recessed within. Pile fine, sparse, and scanty. It is more or less appressed outwardly, except along the inner edge of the occipital recess, where this scanty fringe is directed backward.

The front is quite narrow in the male with parallel sides from the posterior eye corners behind the vertex to within a short distance of the antennae, where it widens slightly. Surface of front and vertex mostly pollinose, plane with the eye margins, except for a very small area above the antennae, which is slightly raised. The ocelli are barely visible in profile and form a long, acute triangle. The upper front and vertex bear 4 or 5 short, scattered hairs, and in the female the lower half of the front has some scanty, suberect pile. Female front about twice as wide as that of the male. Posterior eye margin not quite plane. The proboscis is quite short, relatively stout, somewhat divergent apically with short, rimlike, and conspicuous labellum. Palpus small, short, more or less concealed in the oral recess. Antennae attached at the middle of the head, small and short, the first segment is so short as to form a low, circular, rimlike cup from which the second segment arises. The second segment is very short, about twice as wide as long. Both the first and second segments bear 1 or 2 short, flattened shining hairs at their apices. Third segment about twice as long as the first two segments; the basal half is wide and stout, nearly as wide as the second segment, and this expanded portion is about as long as wide.* The outer half of the third segment is

sharply reduced at the middle of the segment and very much narrower; it ends in a minute spine.

Head, anterior aspect: Head very much wider than the thorax; the antennae are adjacent or at most very narrowly separated. The face is prominent, conically or triangularly peaked and produced forward, often pale yellow in color and with only minute micropubescent along the sides. The genofacial recess is elongate, comparatively shallow in front, deeper behind and below, and confined to the lower fifth of the head. It begins some distance anteriorly to the posteroventral corners of the eye, hence there is a considerable anterior extension of the occiput, which is, however, nearly or quite plane with the eye. The genae are quite nonexistent because of the excessive medial expansion of the eye.

Thorax: The thorax is polished black, very little convex, the mesonotum with scattered, fine, subappressed hairs. Margin and disc of scutellum with a few, fine, long, erect hairs. Humerus chiefly pollinose with only a few minute hairs behind. Metapleuron rather widely long pilose. Metanotum and hypopleuron pollinose. Pteropleuron and sternopleuron without pile but with a little pollen ventrally and posteriorly. Mesopleuron with a dorsal border of fine, erect, slightly flattened hairs. Knob of halteres large and elongate.

Legs: The legs are short and weak, the anterior femur is slightly enlarged basally. Middle and posterior femora with a row of quite fine, moderately long hairs anterovertrally. All of the tibiae lack spicules or bristles but are covered with relatively sparse, appressed, sharp, somewhat flattened hairs. Pulvilli large, broad and rounded, the claws fine, sharp, strongly bent at the apex.

Wings: The wings are hyaline, narrowed at the base and have 2 submarginal cells. The marginal cell is rather wide and still wider near the apex as it is gently curved but swollen backward. First posterior cell widely open, the anterior crossvein lies in the middle of the discal cell. Anal cell extremely widely open, almost fully as wide on the margin as the first posterior cell. Ambient vein complete, the alula absent.

Abdomen: The abdomen is elongate, slender, somewhat laterally compressed in the middle and posteriorly; the ground color is shining black with narrow, pale postmargins to the tergites and the sternites. The pile is sparse and scanty, fine and appressed. There are longer, upright tufts of pile on the first tergite. Male hypopygium bulbous with dististyli concealed.

Material available for study: All three species through the courtesy of Dr. R. H. Painter and Mr. Jack Hall; I have a small series of an undescribed species I collected.

Immature stages: Unknown.

Ecology and behavior of adults: I have collected these flies on two occasions. I took an individual of *Metacosmus exilis* Coquillett in June hovering about a forest path in New Jersey. I have also taken several of these flies of a different species flying in very hot sunshine about clumps of prickly desert plants in the California

desert not far from Desert Center; time, late August. The range of ecological habitats is remarkable.

Distribution: Nearctic: *Metacosmus exilis* Coquillett, 1891; *manipennis* Coquillett, 1910; *nitidus* Cole, 1923.

Genus *Paracosmus* Osten Sacken

FIGURES 112, 119, 360, 619, 896, 897

Allocotus Loew, Berliner Ent. Zeitschr., vol. 16, p. 82, 1872.

Type of genus: *Allocotus edwardsii* Loew, 1872, by monotypy. Preoccupied Fisch., Pisces; Mayr Hemiptera, 1864.

Paracosmus Osten Sacken, Bull. U.S. Geol. Survey, vol. 3, p. 262, 1877. Change of name.

Aethrosia, new subgenus. Type of subgenus: *Paracosmus rubicundus* Melander, 1950.

Melander (1950b), p. 154, key to 4 species.

Small, slender flies easily recognized by the bare aspect and the elongate abdomen, compressed laterally. Like *Metacosmus* Coquillett and *Amphicosmus* Coquillett, the head is subglobular and wider than the thorax; these three genera, together with *Pantostomus* Bezzi and *Tomomyza* Wiedemann, all have not only a wide head but a relatively elongate subcylindrical abdomen; in the three American genera there appears to be a tendency for the abdomen to be more or less compressed. Moreover, in all these genera, and in the strange and very different genus *Peringueyimyia* Bezzi, the occipital lobes are very tightly apposed. Oddly in all five the palpus is extremely long and slender, coiled snake-like, with short apical clublike segment.

In *Paracosmus* Osten Sacken the flies have a very bare aspect due to very short, dense, appressed, setate pile and even some bare and polished areas on face and pleuron. Like *Metacosmus* Coquillett the flies are generally black, largely shining, with pale-yellow postmargins on the abdominal tergites; it differs from the latter genus in the larger head and venation; the anterior branch of the third vein arises as a rectangular crossvein which usually emits a spur directed toward the base of the wing.

In the male of *Paracosmus* Osten Sacken the hypopygium is unusually prominent and protruded and directed obliquely upward.

Paracosmus Osten Sacken is a Nearctic genus that is characteristic of the southwestern United States with some species ranging into Mexico. I have taken the type-species commonly in northeastern Mexico, in Harlingen, Texas, near Beeville, Texas, and in southern California near Pasadena.

Length: 6 to 10 mm.

Head, lateral aspect: The head is more or less triangular, with a moderately produced occiput and a rather peaked and strongly produced front and face. The occiput is dorsally about as long as the third antennal segment and in the middle and below a little longer than the second antennal segment. The part of the occiput is hollowed out into a large, deep cavity. From the outer ridge it slopes sharply forward to the

eye margin. The whole outer surface is densely micropubescent but the pubescence runs in different directions. That part on the upper third or more runs backward and is silvery shining from the lateral aspect. That part in the middle runs forward and laterally, this part allows the brassy black ground color to shine through. Lower occiput thinly pollinose. In addition, along the rim of the central cavity, there is a row of fine, short, erect hairs. The front in both sexes is flat with a very shallow but quite wide transverse concavity or depression deepest across the middle of the front. Surface pollinose with a separated band of fine, erect pile on each side of the front in the male; in the female it is less clearly separated and the color is apt to be different.

The face is peculiar in that the unusually long oragenal cup extends obliquely upward to the base of the antennae and outward almost to the end of the first antennal segment and is demarcated from the lateral face by a crease. Lateral face micropubescent and anteriorly with a row of hairs. Orogenal cup bare, polished, and shining. The eye is hemispherical with the posterior margin nearly plane on the upper half and making a very low, slight bend in the middle and this lower portion gently curved; the postmargin is entire. The proboscis is slender and about as long as the head. Palpus long and slender with a few rather long hairs laterally and at the apex, and with a very small clavate end segment. The proboscis is capable of being rather strongly withdrawn into the head, in some insects it is not as long as the eye. The antenna attached just above the middle of the head, short and relatively small. The first segment is less than twice as long as wide, the second, viewed medially, is as long as wide and slightly wider apically. It has a tuft of stiff setae below on the apical half. The third segment is oval, nearly as long as the first two segments together; it is narrowed briefly at the base, widest on the basal fourth and then narrowed to the truncate apex, and this apex dorsally bears a blunt tubercle or spine. The medial surface of the third segment is covered, except at the extreme base, by a depressed area of micropubescence.

Head, anterior aspect: The head is much wider than the thorax. The eyes in the male are well separated by almost the width of the ocellar tubercle. The ocellar tubercle itself is long and narrow, but the posterior ocelli are set considerably forward near the middle, and the tubercle bears a number of fine, erect hairs of no great length. The female front is not quite twice the width of the male and the ocellar tubercle much lower. The antennae are separated at the base by more than half the thickness of the first segment. The oral opening is quite long, extending from the bottom of the head to the antennae. Interiorly it is rather deep and concave with the lateral wall of the oragenal cup folded inward in the middle with a marked ridge where it ends. The walls of the oragenal cup are moderately sharp throughout lapping over on the lower fourth.

Gena extremely narrow but detectable as a narrow strip along the eye and separated by the tentorial fissure.

Thorax: The mesonotum is low and very gently convex, except in the aberrant species *Paracosmus rubicundus* Melander. The mesonotum has vittae of pollen or coarse micropubescence that is rather conspicuous. Mesonotum also covered with rather abundant, in part dense, appressed, curled, short, wiry pile. Laterally along the side margins the pile becomes longer, still strongly appressed, shining and a little flattened and also curled. Scutellum similar to the mesonotum. Humerus densely micropubescent and rather densely covered with erect pile. Curiously the pleuron is very largely bare and shining, with an oblique or horizontal stripe of fine, pollenlike micropubescence running across the upper sternopleuron and the lower pteropleuron and the whole of the metapleuron. The posterior hypopleuron above the hind coxa is also pubescent. Upper mesopleuron with a narrow band of scanty, curled hairs. Metapleuron with rather dense, long, erect, silvery, flattened hairs and an area of shorter pile behind the hind coxa; another beneath and behind the haltere. Squama short with a fine, short fringe. Haltere relatively small, the knob flattened and concave below.

Legs: The legs are relatively short, the femora are a little thickened but only very slightly enlarged toward the base and the rather longer hind femur is distinctly narrowed and spindly toward the base. Whole tibiae and femora rather densely covered with short, appressed, setate pile on all surfaces, none of it upstanding; the short tarsi are similar. Pulvilli large, as long as the claw. The claws are slightly bent at the apex.

Wings: The wings are hyaline and unusually glassy; the costa and subcostal cells are also hyaline. The marginal cell is strongly swollen near the apex, bent backward, broadly rounded, the second vein meeting the costa at a right angle, or more unusually obliquely backward. The anterior branch of the third vein arises rectangularly, makes a rectangular bend outward at which point it usually has a backward spur and then tends near the apex of the wing to make a sharp bend forward nearly as abrupt as the second vein. The anterior cross-vein enters the discal cell just before the outer fourth. First posterior cell long and very slightly narrowed. Anterior intercalary vein long. The anal cell is widely open, axillary lobe rather narrow, the alula quite narrow and linear. Ambient vein complete.

Abdomen: The abdomen is elongate, at least $1\frac{1}{2}$ times as long as the thorax and rather strongly compressed laterally and black, except in *rubicundus* Melander, and with sharp, pale yellow, bare, posterior margins to all of the tergites, more extensive in the middles and more extensive and wider laterally on the first three. I find 7 tergites, the last one short conical in the female, and in the male there is an eighth tergite laterally. The male, likewise, has a deep, transverse, groove-like depression near the base of the second segment. In the female

it is much closer to the base and less pronounced. The pile of the abdomen is moderately dense, flat-appressed and setate. The sternites have longer and suberect setae. The male terminalia are large, clublike, the dististyli lie on the upper part of the large hypopygium and are extended upward.

The male terminalia from dorsal aspect, epandrium removed, show a rather simplified body, with long sausage-like dististyli which originate a considerable distance back from the basistylus. The epiphallus is split and divided into 2 ejaculatory processes. In the lateral aspect the figure is quite unique, the very large basistylus is almost bowl-shaped, strongly arched beneath, much higher basally. The dististyli that arise from the end of the basistylus are curved upward. The epiphallus and included ejaculatory process are long and rather straight attenuate. Epandrium comparatively long, bluntly lobelike apically.

Material available for study: A considerable series of the type-species and some material of all the known species. I am indebted to Dr. Frank Cole for material of *rubicundus* Melander.

Immature stages: Unknown.

Ecology and behavior of adults: I have collected these flies sometimes rather abundantly resting upon the hot surface of caked sandy places in hot semidesert country; also on sandy banks beside western streams. They rest on the very hot sand in strong sunlight. I have taken them from eastern Mexico, southern Texas, and Los Angeles County, California.

Distribution: Nearctic: *Paracosmus edwardsii* (Loew), 1872 (as *Allocotus*); *insolens* Coquillett, 1891; *morrisoni* Osten Sacken, 1887; *rubicundus* Melander, 1950; *similis* Hall, 1957.

Atherosia, new subgenus

Small, pale flies with comparatively robust uncontracted abdomen; everywhere pale yellow or reddish, including face and frons and only the disc of the mesonotum and the sternopleuron black. Wings water-clear hyaline.

These pretty little flies are related to *Paracosmus* Osten Sacken but differ in the more extensive occiput, the longer, basally tapered third antennal segment, shorter first antennal segment and the vestigial or rudimentary or absent anterior ocellus. Finally in *Paracosmus* and related genera the abdomen is characteristically compressed laterally and the abdomen is narrow, less stout, rather longer.

These flies are regarded as a subgenus of *Paracosmus* Osten Sacken, with type-species *Paracosmus rubicundus* Melander. I want to thank Dr. Frank Cole for providing me with material.

Flies are found in southern California.

Length: 9 mm., including antenna; wing 6.5 mm.

Genus *Peringueyimyia* Bigot

FIGURES 120, 359, 607, 627, 642, 893, 894, 895

Peringueyimyia Bigot, Bull. Soc. Ent. France, ser. 6, vol. 6, p. cx, 1886b. Type of genus: *Peringueyimyia capensis* Bigot, 1886b, by monotypy.

A peculiar genus of medium-sized black flies with more or less drooping head and abdomen. The tergites are linearly margined behind with brownish yellow; their pile is matted and appressed, white or yellowish white. The mesonotal pile is erect, fine, bristly, and chiefly black. All femora and tibiae with spiny black bristles. The proboscis extends beyond the antennae, and the third segment of the latter has a ventral brush of long, yellowish-white pile.

The head is subglobular with the occiput extremely prominent, strongly and convexly sloping backward and inward toward the deep central cavity; the lobes behind the vertex are tightly apposed in contrast to *Nomalonia* Rondani and *Henica* Macquart. The female vertex is much less widely separated and the wing venation is quite different. Glassy hyaline, the wing has 3 tiny brown spots and the anterior branch of the third vein arises as a simulated crossvein with long backward spur vein; the marginal cell is bulbous at the apex.

The single known species is a unique element in the South African bee fly fauna.

Length: 8.5 to 13 mm.; wing: 8.5 to 12 mm.

Head, lateral aspect: The head from the dorsal aspect is subglobular but this is chiefly due to the enormous extent of the occiput, which is about four-fifths as long as the eye itself, and which is strongly sloping and rounded backward both from above and from the side. The halves of the occiput meet closely behind the vertex and form a comparatively shallow but distinct, elongate groove visible from the interior when the head is removed. The occiput is deeply cuplike and there is a linear crease where the two lobes of the occiput are fused above. Pile of occiput scanty, short, rather fine, appressed anteriorly and forming around the rim of the cup an erect, short, sparse fringe. Inner, lower tentorial pits large, deep and obliquely elongate. From the lateral aspect the occiput is greatly reduced in extent below and only about one-third as long as its dorsal length. The front in the female is flattened and has a medial groove; on the upper half it is only as wide as the base of the swollen antennae, and the pile is bristly, comparatively sparse, curled forward; these hairs are not quite as long as the first antennal segment. The front of the male is small, and triangular and bears minute, gray micropubescent only. From the lateral aspect the face is scarcely visible, nonprotrusive and bears near the eye margin a fringe of coarse long hairs merging with similar, equally long, dense pile on the lower half of the first antennal segment. It also continues, though shorter, downward to the beginning of the genae.

The eye is quite large and high, a little shorter below than above, in spite of the fact that the occiput extends farther forward on the dorsal half. The posterior margin of the eye, while not indented, shows a distinct break or bend at the middle, where the occiput expands forward. Eye facets without pile and only slightly enlarged above in the male. The proboscis is extended obliquely upward or forward and is only a little longer than the head and actually shorter when it is extended upward. It is rather slender, with long, slender labellum. Palpus large, elongate, flattened apically, with sparse, bristly hairs laterally, the inner surface particularly flattened and the whole deeply recessed in the oragenal cavity, and consisting of a single segment. The antennae are comparatively small; however, the first segment is swollen, not only below but medially and it is nearly or quite as long as the slender, attenuate third segment. The antennae are separated narrowly at the base; the first segment bears sparse, short, fine, bristly black pile dorsally and on the entire upper half, changing to long, bushy, pale-colored, fringelike pile on the lower half. The second segment is small, short, bead-like, with stubby, black setae above and a few longer, pale hairs below. The third segment is 3 or 4 times as wide on the basal fourth as at the apex; it is never as wide as the second segment; it bears medially a deep, elongate pit on the basal third and the apex is capped with a minute, short, pale, conical spine.

Head, anterior aspect: The head is somewhat more narrow than the thorax, quite circular from the anterior aspect. Eyes in male virtually holoptic for a short distance, the vertical triangle small, longer than wide; the rather small, convex ocelli are not quite equilateral. The oragenal cup is large and extensive, deep above and below. The edge of the cup is rather sharp and linear and separated from the short face by a deep groove completely hidden from the lateral view. This deep furrow leaves the inner margin of the eye strongly sloping and the fringe of pile that ranges down the eye arises from this slope. The genae are reduced to a linear trace by the expansion of the oragenal cup. The lateral furrow extends ventrally into a deep, very narrow, tentorial fissure. Deep inner recess of the occiput almost bare with pollen or minute pubescence only.

Thorax: The mesonotum is a little longer than wide, slightly convex and sloping, especially anteriorly; it is faintly pollinose but subshining and bears comparatively sparse, fine, subappressed pale hairs and equal or greater amounts of fine, erect, not very long, black bristly hairs. The pile becomes more dense, matted, and coarse along the sides and the anterior margin of the mesonotum, where it forms a rather dense fringe cupping around the occiput of the head. Notopleuron with 4 rather long, basally stout, finely tapered, curved, black bristles. There are 6 others that are conspicuous, though more slender, situated above the base of the wing and 3 or 4 still longer bristles curved backward from the postalar callosity. The shining brown scutellum has some short, pale, coarse, curled, appressed hairs, espe-

cially toward the base; there is a border of fine, erect, black, bristly hairs on the outer half and a few at the base and on the lower margin it bears a loose fringe of long, pale, yellowish bristles. The humerus is rather inconspicuous, slightly elongate and convex, and thickly covered with bushy pile. Metapleuron with a conspicuous tuft of pile extending upward and entirely situated above the haltere. Lower metapleuron, hypopleuron, and pteropleuron bare. Upper half and posterior margin of the mesopleuron with much coarse pile, and a small tuft on the upper half of the sternopleuron. Squama semicircular but short with a wide band or fringe of rather dense, fine pile.

Legs: The legs are comparatively long and unusually stout, especially on the femora, yet not swollen. Anterior femur a little enlarged at the base with 4 or 5 short bristles posteroventrally and a similar number anteroventrally and a few, short, appressed, black setae behind intermixed with dense, wide, appressed grayish-white scales. Middle femur with similar scales in front and behind, and similar setae. However, the anterior surface on the outer two-thirds bears along the middle anteroventrally 4 long, basally stout, black bristles, 2 equally conspicuous bristles near but not at the apex, and posteriorly there are 8 outer bristles likewise near the apex. Hind femur with loose, brownish scales and with 10 moderately long, basally stout, apically sharp, posteroventral bristles and on each side near the apex 2 others arranged vertically and quite stout. The anterior tibia bears an anterodorsal and a posterodorsal row of about 12 short, well-developed spines or spicules and posteriorly a row of 6 or 8 spines, 2 or 3 of which are unusually long and stout. Middle tibia with 7 rather long, rather oblique spinous bristles dorsally, 3 or 4 shorter ones anteriorly, 12 or 14 short spines posteriorly and several longer posteroventral spinous bristles. Hind tibia with 4 rows of more sparse spinous bristles, 7 or 8 anteroventrally, 6 anterodorsally and a like number posterodorsally, and likewise ventrally. Pulvilli well developed, tibiae and tarsi with scales, nearly as long as the claw. Claws curved from the base.

Wings: The wings are glassy hyaline; the costal and subcostal cells are pale yellow. The costal, subcostal, and the first longitudinal vein yellow, the remaining veins chiefly dark brown. The wing is large, elongate, not greatly narrowed at the base and there are small, diffuse, blackish spots on the crossveins, especially the radiomedial crossvein and also at or below the extremely short radial sector. There are 2 submarginal cells, but there is a long but quite characteristic spur vein directed backward arising at the end of the basal section of the anterior branch of the third vein. This basal section of the third vein is quite rectangular, simulating a crossvein. The end of the marginal cell is broadly rounded; the second vein is recurrent at the apex. The third vein arises from the second vein very near to the base of the latter, hence the radial sector is extremely short. The anterior crossvein lies rectangularly at the outer fifth of the discal cell. The vein on the

lower side of the discal cell is much more sigmoid than in either *Nomalonía* Rondani or *Henica* Macquart. The first posterior cell is closed with a short stalk and the other half of this cell is triangular. The medial cross-vein at the end of the discal cell is not quite as long as the anterior cross-vein. Anal cell widely open, ambient vein complete, the alula short and narrow with plane margin and nearly as wide apically as basally. The costa is somewhat expanded at the base with weak comb or brush of setae and no hook.

Abdomen: The abdomen is comparatively short oval but narrowing a little apically. Near the end of the third tergite it becomes as wide as the mesonotum and it is rather densely covered with matted, curled, shining, brownish yellow, somewhat flattened hairs, with, in addition, a postmarginal fringe of rather long, shining, slender, brownish yellow bristles. These bristles lie more or less appressed along the abdomen, and laterally along the posterior parts of the segment, there are some long, fine, black, bristly hairs. Ground color of abdomen shining black with the posterior margins yellowish brown. I find 8 tergites in the male, the last two considerably more narrowed, and I find 7 in the female, the last one longer than the preceding ones. Female terminalia with a circle of 5 or 6 blunt, shining, reddish spines on each side apically. Male terminalia only shortly protrusive beyond the last narrow sternite and tergite. The dististyli are apposed, slightly divergent, arising below and turning upward. The hypopygium is thus reversed in position. The last tergite, which Hesse (1938) states is the last sternite, is notched in the middle. Dististyli elongate and flattened with sharp apex and flared subapically.

Material available for study: I am deeply indebted to Dr. A. J. Hesse for furnishing material of this genus.

Immature stages: Unknown. However, the spiny armature on the female genitalia suggests that the eggs are laid in the soil.

Ecology and behavior of adults: I have seen no recorded comment on the behavior of adults or the flowers they visit.

Distribution: Ethiopian: *Peringueyimyia capensis* Bigot, 1886.

Genus *Neosardus* Roberts

FIGURES 121, 398, 621, 639, 900, 901, 902

Neosardus Roberts, Proc. Linnean Soc. New South Wales, vol. 54, p. 560, 1929. Type of genus: *Neosardus principius* Roberts, 1929, by original designation.

Roberts (1929), p. 560, key to 4 species.

Strange flies of small to medium size, robust in form and at once peculiar in the extraordinary width of the front, vertex, and inflated face. The antennae are strikingly elongate, cylindrical, and relatively slender. The wings have a brown pattern. All species seem to have emerald or malachite green scales on the thorax. The

wing has 4 submarginal cells. Finally, it is to be noted that although the occiput is shallow and short laterally and dorsally, it is definitely bilobate, and it has a deep central cavity. There are no closely related genera. It must be regarded as a member of the Cylleninae, which is relatively generalized with respect to the occiput and highly specialized in the matter of the front and face and antenna.

This genus is only known from Australia but is found on both sides of the continent.

Length: 6.5 to 12.5 mm.; wing, 5.5 to 10 mm.

Head, lateral aspect: The head is more or less subglobular, very strongly inflated, in consequence of which the eye appears to be somewhat reduced although the eye is not small. The occiput is not at all extensive from the lateral aspect, except below, where in some species it is even more pendulous than in *Nomalonía* Rondani, and thus there is considerable variation in this respect. The occiput from a posterior aspect shows a deep, cuplike depression such as is characteristic of the Cylleninae; nevertheless its area is central and small so that the outer part of the occiput laterally between the recess and the eye margin is very broad, moderately convex, gently sloping from the middle to the eye margin, and the halves, while bilobed above, have a usually wide or deep sulcus behind the ocelli. In some respects these features and the long, slender antennae suggest a remote derivation from the Bombylinae. The pile of the occiput is fine, erect, and rather scanty and becoming stiff and almost bristly on the upper fourth near the vertex. The eye is comparatively long compared to the type, hemispherical in front, strongly rounded below with the posterior margin approximately plane only over the middle of the head. The front is extremely wide even in the male of the type-species where it forms a large triangle, widely divergent below, everywhere pilose, and covered with quite long, loose, scattered, rather fine hairs, except along the eye margin. In *Neosardus paramonovi*, new species, it is even wider, inflated shining yellow with loose, scattered, erect, bristly hairs and the whole translucent. In the type-species and in *Neosardus paramonovi*, new species, each side of the face is considerably wider than the eye, its width extraordinary, and its sides parallel.

The oragenal cup is rather strongly developed, but laterally its wall on the upper half is very broad, gently sloping and convex, and demarcated from the face and genae by a rather distinct crease or fissurelike sulcus, which never descends into a deep, slitlike, tentorial fissure as in *Henica* Macquart. This creaselike fissure extends to the base of the antennae so that the upper medial wall of the oragenal cup is long and convex and this part of the face bears a tuft of bristly hairs beneath the antennae. Outer wall of the oragenal cup without pile, except beneath the antennae, but the extremely broad space between the furrow and the eyes and the equally extensive genae below bear numerous, long, fine, erect, stiff, scattered hairs, which are pale in color. The proboscis is quite elongate and slender and twice as long

as the head. It originates at the extreme rear of the head almost behind the eye. The labellum is long, microspinulose. Palpus slender, elongate, and clearly composed of 2 segments, the apical segment short, and the whole palpus bearing scattered, fine hairs of no great length. The antennae are attached at the upper third of the head and are elongate and slender; the first segment is especially elongate, cylindrical, twice as long as the second segment, which is nearly the same width. Both of these segments bear appressed setate hairs dorsally and ventrally. Third segment with disclike rim at the base, not quite as wide as the second segment, rapidly widening to the middle, then more narrow to the apex, which may or may not bear a short microsegment but in any case has a minute apical spine. The third segment is nearly or quite as long as the second segment.

Head, anterior aspect: The head is much wider than the thorax. The eyes in the male are widely separated by a distance slightly greater than the ocellar tubercle. The ocellar tubercle is prominent, rather swollen, obtuse, with all 3 ocelli large, the posterior pair almost touching the eye margin, and the tubercle bears a tuft of long, fine hairs, sometimes bristly, which stand erect. The oral opening is relatively small when compared to the width of the face and it is relatively shallow with its inner wall sloping as much as its outer wall. The genae are excessively wide in consequence of the extraordinary width of the face.

Thorax: The thorax is only slightly convex; the mesonotum is black in ground color, thinly pollinose, and rather densely covered in many species with emerald green or coppery scales. The scales are rather limited in the type-species. The humerus, lateral margin, and the apical half of the scutellum and the whole pleuron in some species are light-brownish orange. In the type-species the whole thorax is blackish, with rather dense, gray pollen. Notopleuron with 2 or 3 long, slender bristles, postalar callosity with 1 or 2, and the scutellar margin with 2 or 3 pairs of bristles. Metanotum and metapleuron bare, upper posterior hypopleuron below the haltere with a patch of pile. Pteropleuron pollinose only. Mesopleuron rather densely and sternopleuron rather scantily pilose.

Legs: The legs are slender and rather short. Anterior femur with fine pile only. The type-species has fine pile only on the remaining femora but in other species with 3 or 4 slender bristles ventrally on these last 4 femora. Anterior tibia with a few minute spicules, 10

or 12 anterodorsally, 3 or 4 posterodorsally, or in the small, delicate type-species these spicules at the most are represented by short, stiff hairs. Bristles of hind tibia present in 4 rows of 4 to 6 elements, all slender and of no great length. Pulvilli slender, but not as long as the claws, which are fine, sharp, and gently curved.

Wings: The wings are largely mottled with brown with some clear areas along the posterior border, sometimes at apex of wing. Auxiliary cell often clear and a large hyaline spot distally in the second basal cell. First posterior cell widely open, discal cell short or long, and the anterior crossvein lying at the middle of the discal cell. Ambient vein complete; alula hemicircular.

Abdomen: The abdomen is elongate in the type-species, and only the base of the abdomen is as wide as the thorax. In some other species the abdomen widens beyond the base, is oval and drooping, and wider than the mesonotum. Color black, shining, and somewhat metallic, or in other species shining orange brown or with black spots or vittae medially. The pile is rather scanty, erect, and short, or may be appressed, fine and bristlelike and short. First abdominal segment with a rather dense brush of rather long, erect pile laterally. Hypopygium partly recessed, the long basal lobes adjacent, the dististyli concealed by curled hairs from the last sternite.

Material available for study: Two species, the type-species, given me by the late Dr. A. J. Nicholson of the CSIRO, and a larger, undescribed species collected by the author in Western Australia, here illustrated and named in honor of Dr. Paramonov, who truly liked the bee flies, and to whom we are all indebted for his astute observations.

Immature stages: Unknown.

Ecology and behavior of adults: Very little is known about the ecology of this genus. In January 1954, I collected a female of a large species resting on hot, sandy ground amid weeds, grass, and herbs in Western Australia near Bull Pond out from Perth. It was a sunny day with a very strong wind blowing. Females have a well-developed fringe of spines around the ovipositor, clearly suggesting that the eggs are deposited in soil.

Distribution: Australian: *Neosardus circumdatus* Roberts, 1929; *lepidus* Roberts, 1929; *nigratus* Roberts, 1929; *paramonovi* Hull, new species; *principius* Roberts, 1929.

Subfamily Lomatiinae Schiner, 1868

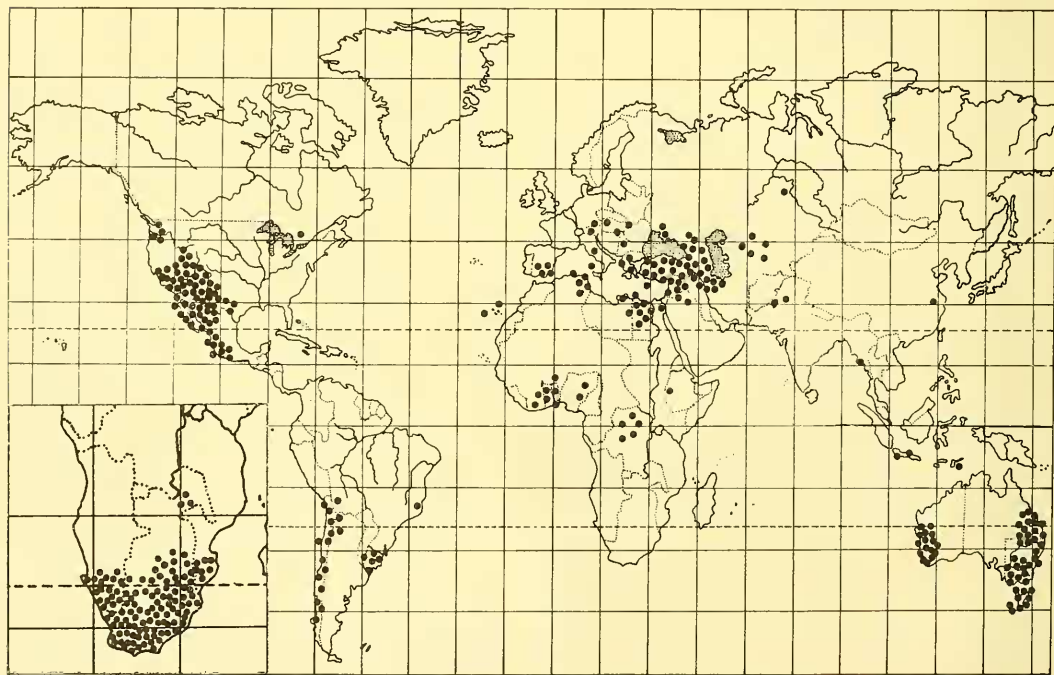
In the Lomatiinae we find several characteristic tribes. The Lomatiini are best developed in the Old World, especially southern Europe and South Africa. The Comptosini are greatly concentrated in Australia and in the Chilean subregion of the neotropics, areas to which they are restricted and where there are many species. I believe the troublesome group of genera centered around *Xeramoeba* Hesse and *Petrorossia* Bezzi are annectant, though distant, with the subfamily Anthracinae; we find that not only is the manner of origin of the second vein highly variable but so is its point of origin. The squamal fringe in the tribe Xeramoebini and throughout the whole subfamily is composed of only fine, soft hairs; the relationship between the genera in this tribe and certain genera in several other tribes is so close as to almost amount to hair-

splitting. From a comparative study of more than sixty characters within virtually all of the known genera of the subfamily, I conclude it is necessary for a preservation of values to reduce the subfamily Aphoebantinae to tribal rank and to separate other distinct groups as tribes. I have not seen the genus *Edmundiella* Becker. Tribal characters are set forth below:

Tribe Lomatiini

This tribe is characterized by indented eyes, with or without a bisecting line. The metanotum is pilose without exception, but bare within 15 other genera in other

LOMATIINAE



TEXT-FIGURE 43.—Pattern of the approximate world distribution of the species of the subfamily Lomatiinae.

tribes, and in this tribe the metapleuron in front of the haltere may or may not have a tuft of pile. The second vein is basal in origin and arises gently, that is, acutely. The gena is shelving inward. The marginal cell is at most slightly widened and often ends obtusely, and the second vein ends at right angles but may end even acutely; hence there is no radial loop. One or two Australian species do have a slightly protrusive marginal cell, but yet are far from the radial loop found in the Comptosiini; see figure. The tribe contains *Lomatia* Wiedemann and its subgenera. It also contains *Anisotamia* Macquart, *Ogcodocera* Macquart, and *Bryodemina* Hull. I also place *Edmundiella* Becker here.

Myonematini, new tribe

This tribe is erected for the unique genus *Myonema* Roberts, which I believe more properly belongs within the Lomatiinae. The eyes are indented, the genae are shelving inward, which is an important character of Lomatiinae, and finally not only are the ocelli set very far forward indeed, but there is an extraordinarily deep, curious, fossa or trench between the eyes posterior to the ocelli.

Antoniini, new tribe

Here the eyes are indented and bisected, but there is no postocellar fovea or trench. The ocelli are placed posteriorly; the genae shelf inward but are very narrow. The front is strongly protuberant; the eyes have a unique, strong, greenish to reddish reflection. There are 3 submarginal cells, the first posterior cell is closed and stalked, and more important the anterior crossvein is at the outer tenth of the discal cell. It contains the one genus *Antonia* Loew, a partial mimic of such flies as the syrphid *Xanthogramma* Schiner. It is perhaps more correct to call this a parallel development.

Tribe Aphobantini

A group in which the eyes are both indented and bisected, but its principal distinguishing characteristics are the short, vertical or retreating, nonconical, non-hoodlike face together with the gentle, acute origin, and basal position of origin of the second vein; the third vein arises from the second vein, dipping downward, swollen, and often with a knotlike swelling at point of origin. The metanotum is bare. Contained are the 4 genera: *Aphobantus* Loew, *Pteraulax* Bezzi, *Epacmus* Osten Sacken, and *Pteraulacodes* Hesse. Male terminalia terminal, large, and of considerable size.

Tribe Prorostomatini

In general appearance a group of flies not greatly dissimilar to *Aphobantus* Loew. Both have the eyes indented and bisected. However, they are very distinct in three particulars. The second vein arises abruptly with rounded curve, and its point of origin lies between the base of the third vein and the anterior crossvein, rarely close to the crossvein; the metanotum is pilose in all the included genera, except the European type-species of *Plesiocera* Macquart. Included are *Prorostoma* Hesse, *Conomyza* Hesse, *Stomylomys* Bigot, *Exepacmus* Coquillett, *Eucessia* Coquillett, *Epacmoides* Hesse, *Coryprosopa* Hesse, and *Plesiocera* Macquart.

Xeramoebini, new tribe

The second vein arises abruptly though with rounded base; its point of origin is rather close to the anterior crossvein. The face is short, not conical or hoodlike. The proboscis is short and contained within the oral cavity and the labellum muscoidlike. The metasternum is bare. A plumula is present (in *Xeramoeba* Hesse and *Chionamoeba* Sack), or absent. Contained are *Petrorossia* Bezzi, *Desmatoneura* Williston, *Xeramoeba* Hesse, *Chionamoeba* Sack, and *Chiasmella* Bezzi.

Tribe Comptosiini

These are large flies confined to Australia and southern South America. Without exception all have the metanotum and the upper hypopleuron pilose. The South American *Lyophlaeba* Rondani, and all of its subgenera, including *Macrocondyla* Rondani, are sharply distinguished from the Australian *Comptosia* Macquart, and its subgenera by the dense tuft of pile upon the metapleuron. The separate *Ylasoia* Speiser and *Doddosia* Edwards do not follow this rule. All these genera in this tribe have a protrusive, expanded, finger-like or otherwise complex marginal cell. Submarginal cells range from 2 to 4 with those genera having 4 such cells certainly representing the more archaic forms of these relict genera. In Australia I have collected annectant species of *Lomatia* Meigen that merge into *Comptosia* Macquart, but I have collected only females.

In this subfamily the hypopygial figure is characteristically elongate and slender in contrast to the conspicuously widened base found in the Exoprosopinae. Also, the epandrium is rather characteristic, being elongately triangular, therefore rather narrowed in terms of maximal width of thickness. Quite often it is lobed or sharply angulate dorsobasally and almost al-

ways with a prominent, sometimes quite conspicuous, narrow, basiventral, downturned lobe or extension. Again the dististylus is usually quite large, rather elongate, upturned, with pointed but not incised or hooked

apex. An outstanding exception, to this general character in the subfamily is the genus *Epacmus* Osten Sacken, which fits none of the above descriptions. Possibly *Epacmus* belongs in the Cylleniinae.

KEY TO THE GENERA AND SUBGENERA OF THE LOMATHINAE

1. The second vein arises abruptly and at right angles or almost at right angles to the third vein, stem vein, but with the curve broadly rounded, usually at some point between the base of the discal cell and the anterior crossvein, rarely opposite the base. Squama always with soft, fine-hair fringe only; scales absent. Antennal style never with a well-developed whorl or brush of hairs at apex, 2 or 3 submarginal cells present. Proboscis quite short and contained within the oral cavity 2
- The second vein arises gently at or before the base of discal cell and always at an acute angle. Squamae likewise without scales on margin. Two to 4 submarginal cells present 16
2. Wing with 2 submarginal cells 3
- Wing with 3 submarginal cells 14
3. Middle of posterior eye margin without a distinct concave indentation or concavity, and without any medial fissure or groove on the middle of eye. Upper half of eye margin anteriorly receding leaving the occiput prominent. Face obliquely conical, hoodlike. Plumula present, but weak 4
- Middle of posterior eye margin with a distinct indentation or concavity of varying depth, and with or without an accompanying horizontal fissure or groove on the middle of eye. Upper half of posterior eye margin sometimes recessive to a varying degree, or not at all receding 5
4. Face produced and bluntly rounded in front, not extending to the apex of the antenna or beyond it. Surface of face pollinose with dense, short, appressed, stiff pile. Anterior branch of third vein arises gently in an arch.

Prorostoma Hesse

Face strongly produced and peaked, rounded above, plane on the oragenal cup and face extended well beyond the apex of the antenna. Surface of face polished, with scattered setae. Anterior branch of third vein arises gently. Second vein arises rectangularly as a simulated crossvein with basal spur *Coryprosope* Hesse

5. Front strongly swollen; face also bulging forward, at least on the upper part. Face vertical or receding, not extended beneath the antenna; not peaked, hoodlike, or conical. Xeramoebini 7
- Front not swollen 6
6. Face very short, both vertically and horizontally, even at base of antenna 8
- Face distinctly produced below the antenna, prominent, rounded in front or peaked and conical 10
7. Face vertical, the oragenal cup separated from the face by a distinct sulcus. Front of male with dense mat of subappressed silver or golden micropubescence. Abdomen slender and tapered. Anterior tibia with minute bristles.

Desmatoneura Williston

Face shorter and retreating below, the oragenal area not separated. Front with longer pubescence but not matlike or extraordinarily dense. Abdomen shorter, wider at base. Anterior tibia with slender spicules. Plumula present. Labellum muscoidlike *Chionamoeba* Sack

8. Third antennal segment onion-shaped, the short style thickened and the microsegment with a crown or circlet of a few long hairs at the apex, and also an apical spine; plumula present; in other respects differing in only specific characters from *Petrrossia* Bezzi. Proboscis-labellum of muscoid type (*Xeramoebini*).

Xeramoeba Hesse

Third antennal segment more conical, longer, the style more slender, the apical spine at end of microsegment without a circlet of long hairs. Plumula absent 9

9. Anterior crossvein at least midway between base and middle of discal cell. Abdomen broad at base and elongate oval, without scales. Alula and squamae short but distinct. Pile of front and face dense and soft and rather long. Eyes well separated. Metanotum bare. Apex of third segment often with a pencil of hairs and a style. Beaked dististylus produced into a short twisted or curved, or scroll-like process *Petrrossia* Bezzi
- Anterior crossvein quite at the middle of discal cell. Abdomen elongate, slender, cylindrical, covered with scales. Eyes approaching closely in both sexes. Alula and squama greatly reduced. Metanotum pilose.

Petrrossia (Pipunculopsis) Bezzi

10. Face strongly produced but bluntly rounded. Antennae set quite far apart, separated by at least their own length. Proboscis confined to the oral recess; second vein arises a considerable distance proximal to the anterior crossvein. Squama with only flattened hairs. (See Exoprosopinae.)

Synthesia Bezzi

- Antennae not widely separated. Face either conical or with liplike extension 11
11. Proboscis distinctly extended beyond the face. Second vein arises at the anterior crossvein, sometimes slightly before or after. Squama with a fringe of hair.

Chiasmella Bezzi

- Proboscis contained within the oragenal recess 12
12. Alula greatly reduced, the axillary lobe narrow. Orogenal cup rather conical and peaked, or triangular, but not extending beyond the antenna. Indentation of posterior eye margin usually deep and conspicuous 13
- Alula well developed; axillary lobe wide. Orogenal cup prominent but shorter, more rounded and convex dorsally and bearing appressed scaliform pile. Indentation of eye margin weak and shallow. Anterior branch of third vein simulates a crossvein. Pile of the tapered, cylindrical, compressed, slender, elongate abdomen is largely appressed and scaliform in character *Epacmoides* Hesse
13. Occiput rather long behind the ocelli, the fissure deep and narrow, the lobes almost or quite touching. Much erect, long, dense pile present anteriorly on mesonotum and anteriorly on base and sides of the abdomen.

Plesiocera Macquart

Occiput short, not extensive behind the ocelli, the fissure wide and correspondingly shallow *Conomyza* Hesse

14. Proboscis twice as long as head or longer. Alula absent or nearly so and axillary lobe narrow. Anterior margin of wing blackish, the black margin irregular behind. Face conical and with scales, the sides not converging below. Sides of abdominal tergites with scales, the abdomen relatively broad and oval. The second vein arises abruptly midway between base and middle of discal cell. Last section of second vein gently sigmoid at base, more strongly sigmoid apically. Squama with only flattened hairs. (See Exoprosopinae) *Isotamia* Bezzi
- Proboscis not extending beyond the apex of face. Alula and axillary lobe well developed 15
15. Middle of posterior eye margin with a deep, conspicuous indentation together with accompanying horizontal, anterior, fissure. Anterior tibia without spicules. Face conical and extending beyond the antenna.

Stomylomyia Bigot

Middle of posterior eye margin with a shallow indentation. Face conical, extending at least to end of antenna. Second vein arising midway between base and anterior crossvein of discal cell. Indentation of posterior eye margin quite shallow *Exepacmus Coquillett*

16. Second vein with a strong radial loop giving the marginal cell a protrusive, fingerlike ventroapical lobelike form of varying prominence. Hence the second vein is strongly recurrent. Two to 4 submarginal cells present. Wings elongate and slender, the base and axillary cell either wide or whole base of wing sometimes greatly narrowed; wings usually banded or wholly brownish or veins suffused and apex sometimes chalky white in some groups, especially in males. Orogenal recess extending almost or quite to the base of antenna. Flies which are rarely less than medium size; these flies usually large and often very large. Abdomen usually elongate with only a slight taper; it is only rarely broad, wide, and flattened and such species are relatively flat with lateral, flattened tufts of pile on the tergites. Metapleuron in front of halteres bare, or pilose. Male genitalia always small and recessed within and overlapped by the hoodlike seventh and eighth tergites. Comptosini 32

Marginal cell at most broadened apically, the end obtuse, gently rounded or acutely angulate, the second vein meeting costa usually approximately at a right angle; apex of marginal cell commonly gently swollen below like the end of a finger. In this division the flies are either small, with obtusely tapered and narrowed or even laterally compressed abdomen with large conspicuous terminal male genitalia, and wings vitreous hyaline, rarely tinged, or flies are larger, with wider abdomen with nearly parallel sides and wings clear, basally infuscated, or suffusedly clouded, banded, or spotted. Male genitalia smaller and visible only from below. Metapleuron in front of haltere either pilose or bare. A few giant species have a very wide abdomen, either flattened, with lateral tufts or pile or a convex abdomen with bushy pile laterally and posteriorly. Orogenal recess not extending to the base of the antenna 17

17. Small, slender flies for the most part; abdomen elongate and gently tapered or occasionally short oval; abdomen sometimes compressed through the middle. Male genitalia usually large, terminal, and conspicuous leaving the apex of the abdomen obtuse. Wings hyaline or rarely brownish, yellowish, or smoky at base 18

Flies of small or large size; usually medium sized but occasionally very large and such giant species usually have conspicuous tufts of long pile in front of the haltere. Whole thorax including scutellum, always black or brownish black. Abdomen usually as wide as the thorax or wider and oval and often with bright, shining yellow postmarginal bands on the tergites; tergites thinly covered with fine, more or less erect pile or with post marginal bands of either straight or curled golden, flat-lying hairs; lateral margin of abdomen with fringe of uniformly colored pile either yellow or black or of alternating colors, sometimes formed into conspicuous flattened tufts. Male genitalia of the more or less recessive and concealed type, larger than in Comptosini but much smaller than the Apoebantini and nonterminal in type. Lomatiini . . . 25

18. Three submarginal cells 19
Two submarginal cells 21

19. Anterior crossvein enters the discal cell almost at the end of this cell. Wing very long and slender, about 4 times as long as wide. Anal cell widely open. First posterior cell closed and with a long stalk. Radial sector vein scarcely evident, the junction of veins almost pointlike. Front of these flies swollen and face peaked forward into a long cone of varying extent. Much opaque or feebly shining canary-yellow color on head, thorax, and abdomen (*Xanthogramma Schiner* mimics); abdomen moderately

elongate, with more or less parallel sides and lateral tergal margins scalloped or crenulate. Male terminalia rather large. Male eyes separated. Antonini.

Antonia Loew

Not such flies. The anterior crossvein enters the discal cell at, near, or before the middle. Male eyes holoptic . . . 20

20. First posterior cell closed with a distinct stalk or petiole. Male genitalia large, terminal, obtuse. Face in lateral aspect only slightly convex or tumid, the hair upon it equally dense or distributed all over its surface and not confined to an apical brush. The first antennal segment is longer and not eupleike; third antennal segment distinctly more quickly broadened basally, therefore the base more bulblike, or onion-shaped. The vestiture of the front, face, and antenna is longer and denser and takes the form of erect, bristly hairs. Bristly hairs on the hind margins of the tergites long, erect, prominent especially on last segments of both male and female. Hind femur comparatively stout, with prominent bristles below, especially in males. Squama large, broad, earlike . . . *Pteraulax Bezzi*

First posterior cell open. Squama poorly developed. Face in lateral aspect more subconically prominent, the apical part of the orogenal cavity deep and the apical part of the face appearing to project over it due to the presence of a conspicuous brush or dense tuft of bristly hairs across apex of face; the remainder of the face without long hairs. The first antennal segment is distinctly shorter and cup-shaped; third segment more gradually broadened basally, more conical, hence the base not bulblike. The vestiture of the front consists of short hairs, still shorter and more sparse on the antenna. Pile of face sparse and short; most of face and front with dense cover of flattened scales. Bristly hairs across hind margins of tergites poorly developed *Pteraulacodes Hesse*

21. Proboscis long and slender, distinctly extending beyond the apex of the oral cavity and thrust upward except when feeding. Third antennal segment bulblike at base. Suddenly constricted into a slender, columnlike style with small bristle-tipped microsegment twisted or hooked upward or sideways. Face protruding below; genae narrow, oral opening elongate. Labellum slender, corneous.

Epacmus Osten Sacken

Proboscis almost always contained within the orogenal cavity at or most barely extended beyond; labellum enlarged, fleshy, muscoidlike. Third antennal segment pyriform, conical or whole apical part thickened, sausage-like. Face vertical, more usually retreating. If hoodlike and projecting see *Plesiocera* Macquart 22

22. Third antennal segment evenly and regularly conical, little longer than wide and gradually narrowing. The apex is capped with minute, bristle-tipped microsegment. Proboscis barely extends beyond oral recess, the labellum fleshy. Abdomen short oval. Face bare above. Coloration of type-species light red. Circular margin of upper face bears a fringe in one row of strong red bristles. Middle of first tergite strongly depressed.

Eucessia Coquillett

Third antennal segment distinctly constricted subbasally and distinctly longer than wide. Third segment of varying length and width especially with respect to the narrowed part 23

23. Third antennal segment bearing a two-segmented style, the second segment tipped with a bristle.

Apoebantus (Cononedys) Hermann

Third antennal segment with a one-segmented style . . . 24

24. Vestiture of abdomen composed of abundant scales of rather slender form, or flattened, appressed hairs; hairs sparse. Metapleuron in front of haltere bare. Vestiture consists mostly of rather densely appressed scales or hair and is alike in the two sexes *Apoebantus Loew*

Vestiture of male abdomen, less so in females composed of abundant, long, very fine, erect, usually pale or whitish

- hair. Few or no scales present on body. Vestiture of males and females, however, often different. Metapleuron in front of haltere with appressed tufts of fine twisted pile *Aphoebantus* (*Triodina*, new subgenus)
25. Metapleuron in front of haltere bare; at most covered with pollen 26
- Metapleuron in front of haltere with a distinct, conspicuous tuft of soft pile or bristly hair 29
26. Wings very long and slender, at least twice as long as the abdomen. Only 2 known genera and 2 known species included here 27
- Wing at most $1\frac{1}{2}$ times as long as the abdomen. Many species in Europe and South Africa included 28
27. Wings and whole fly quite large. Wings uniformly brown. Third antennal segment small but much constricted at the base and onion-shaped, the stylar portion long. Whole insect gray pollinose. A single species from Canary Island. *Lomatia* (*Canariellum*) Strand
- Small, gray flies not or scarcely more than 6 mm., in length. *Edmundella* Becker
28. First posterior cell closed and stalked. Unusually large, flies with straw-yellow pile and reddish-yellow antenna. Venation typically like *Lomatia* Wiedemann; the base of the anterior branch of the third vein arises rectangularly at least in some individuals and there is a stump vein. Genus monotypic *Anisotamia* Macquart
- First posterior cell open though sometimes characteristically narrowed especially in South African species. Wings clear with anterior border smoky to the middle or with a suffused middle band; abdomen shining black with sulphur-yellow postmarginal bands on the tergites, which are sometimes interrupted. South African species with wings sometimes spotted, the abdomen black with postmarginal fascia of appressed golden hair; wings usually banded. Flies of medium to large size. Anterior crossvein enters the discal cell well beyond the middle . . . *Lomatia* Meigen
29. Giant flies with strongly convex abdomen and bushy pile laterally and posteriorly, or short pile and long flat tufts laterally. Third antennal segment long conical and slender. Proboscis short, the labellum large. First posterior cell greatly narrowed or closed and stalked 30
- Quite small flies, with flattened abdomen, only slightly convex. Pile fine, erect, sparse dorsally on abdomen, with conspicuous lateral border of pile, flattened into a mat, and again at apex of abdomen. Genitalia minute. First posterior cell open maximally. Third antennal segment short conical *Ogcodocera* Macquart
30. First posterior cell closed and stalked. Proboscis slender throughout but labellum leaflike. Lateral pile all black and discal pile black except pinkish posteriorly at apex of abdomen. Very large, robust flies. *Bryodemina* Hull, new genus
- First posterior cell greatly narrowed. Large flies with strongly flattened, broadened abdomen, the pile appressed, black, except on postmargins and part of tufted, flattened, lateral border where it is yellow. Proboscis expanded distally and the labellum quite fleshy and muscoidlike. *Bryodemina* (*Brachydemina*, new subgenus)
31. Small flies of about 8 mm. length with quite slender, compressed or subcylindrical abdomen and very large subglobular head. Femora and tibiae with only soft, minute, short, fine, more or less appressed pile. The anterior branch of the third vein arises by a subrectangular, simulative, false crossvein, or as in the type-species arises as an abruptly rounded arch. Wing narrowed at base, vitreous hyaline, the alula absent, the anal cell and first posterior cell widely open; second vein strongly recurrent at apex. Males dichoptic, very narrowly, but with parallel sides; ocelli set extremely far forward as in *Myonema* Roberts but with no deep trench or fossa behind the ocelli as in that genus. (See Cylleninae.) *Docidomyia* White
- Not such flies 32
32. Metapleuron in front of haltere bare 33
- Metapleuron in front of haltere with a distinct tuft of long, fine hair or bristly pile 42
33. A tuft of bristly hairs on the lower posterior corner of the pteropleuron. Metanotum bristly pilose laterally, the plumula wanting. Third posterior cell very much narrowed on the wing margin 45
- Without such a tuft of bristly hairs on the pteropleuron. Third posterior cell not conspicuously narrowed 34
34. Alula quite large and anal vein sinuous. Large flies with very wide, short-oval, shallowly convex, dull, short-pilose abdomen, the tergites with prominent, flattened tufts of rather long pile. Third antennal segment long and attenuate. Wings maculate *Oncodosis* Edwards
- Alula either reduced or absent. Anal vein straight 35
35. Alula completely absent. Male eyes narrowly but distinctly separated. Wing markings form a special type; chalklike bands never present in either sex; second section of third branch of the medius as long or usually longer than the first; fourth branch of radius more strongly recurved and the upturned part distinctly and characteristically sinuous. Axillary lobe quite narrow. Three submarginal cells. *Comptosia* (*Aleucosia*) Edwards
- Alula present. Male eyes usually in contact. Axillary lobe not reduced 36
36. Two submarginal cells 39
- More than 2 submarginal cells 37
37. Four submarginal cells. Wings with a clear apical non-chalky band and a clear band across the middle. Axillary lobe wide, alula clearly present, excluding *plena* Edwards. *Comptosia* (*Epidosia*, new subgenus)
- Three submarginal cells 38
38. Wings speckled and clouded; medium-sized, usually blackish flies, in which the veins evidence a tendency to stubs, becoming very advanced in *norrisi* Paramonov, the selected type of *Chelina*. Alula present. Proboscis slender, distinctly longer than the oral cavity; labellum small, slender, corneous. Third antennal segment sagittate, the true style short . . . *Comptosia* (*Chelina*, new subgenus)
- Large flies, the color generally dark brown or even light red; scutellum generally red. Wings long and reddish brown or rufous, sometimes wholly reddish; often with chalky white apical or preapical band, accompanied by an elongate, red, black-vittate abdomen and micronodulate costa, or very large species with short-oval, blackish abdomen modified by dense, curled appressed pile and a pilose vitta and fasciate bands. The costa of wing sometimes micronodulate. Alula present, axillary lobe wide. Antennae always sagittate. Male eyes touching or separated *Comptosia* Macquart
39. Antennae distinctly sagittate or spearlike. Large flies with more or less strongly developed bands of brown upon the wings. Axillary lobe well developed. Alula present. *Comptosia* (*Alyosia*) Rondani
- Antennae bulbiform, the basal bulb of third segment small, the abruptly formed style long and slender 40
40. Anterior branch of third vein arising very close to the end of the discal cell. Small species with dark brown wings in which there are a few clear spots. Alula present. Axillary lobe only moderately narrowed. Proboscis extends beyond oral cavity; labellum short, slender. Species: *feneestrata*, new species. *Comptosia* (*Opsonia*, new subgenus)
- Anterior branch of third vein arising far beyond the end of discal cell 41
41. Large flies with broad abdomen wider than the thorax, convex, more or less decumbent; wings large with two distinct brown crossbands and remainder of veins more or less suffused. Alula quite wide. No lateral mats of flattened pile upon the abdomen and wing not narrowed apically, the base greatly widened and anal vein only slightly sinuous. Species: *duofasciata*, new species. *Comptosia* (*Paradosia*, new subgenus)

Small to medium-sized flies with elongate-oval abdomen, blackish, rather uniform in color and wings barely smoky subhyaline except on the anterior border, which is more blackish. Proboscis contained within the oral cavity; labellum large, muscoidlike, sometimes longer than the the basal stem. Species: *casimira*, new species, figured.

Comptosia (Anthocolon, new subgenus)

42. Metapleuron with a strongly developed tuft of long, fine pile in front of the haltere. Two submarginal cells. Radial loop short, alula present; posterior part of wing entirely hyaline, except for a diffuse light-brown middle band; 2 of these bands, the basal and the apical are incomplete. Abdomen elongate, with parallel sides; antennae sagittate, male eyes touching. Proboscis stout and shorter than the head, barely extending beyond the oral cavity.

Doddosia Edwards

More than 2 submarginal cells. Proboscis long and slender; always longer than the head. (*Lyophlaeba* Rondani, including subgenera *Macrocondyla* Rondani and *Compella* Hull, new subgenus) 43

43. Four submarginal cells present and the third antennal segment, long, conspicuous, flattened and swordlike. Pulvilli vestigial, stublike ***Lyophlaeba Rondani***
Three submarginal cells. Pulvilli well developed. Third antennal segment spikelike, long slender and attenuate. 44

44. First posterior cell undivided.

Lyophlaeba (Macrocondyla) Rondani

First posterior cell divided by a crossvein.

Lyophlaeba (Compella, new subgenus)

45. Long winged, black flies, the mesonotum yellowish vittate. Wings with quite blackish bands, the hyaline areas with chalk-white villi. Wing of normal shape at apex. Radial loop long. Two submarginal cells present. Third posterior cell long but narrowed apically . . . ***Ylasoia Speiser***
Reddish-brown flies with dense, very short, bristly, reddish pile; appearance rather bare. Apex of wing distinctly hook-shaped. Wings hyaline with complex pattern of reddish sepia. Three submarginal cells and radial loop short; third posterior cell short, rounded, and club-shaped above, narrowed below . . . ***Ulosometa Hull, new genus***

Genus *Lomatia* Meigen

FIGURES 130A, 139, 144, 145, 146, 216, 354, 701, 733, 903, 904, 905

Stygia Meigen, Systematische Beschreibung, vol. 2, p. 137, 1820.

Type of genus: *Bibio sabaea* Fabricius, 1781, designated by Becker, 1913a, p. 460, but given as *Lomatia sabaea* Fabricius. Preoccupied by Latreille, Lepidoptera, 1804.

Lomatia Meigen, Systematische Beschreibung, vol. 3, Vorwort, 1822. Change of name. Type of genus: *Bibio sabaea* Fabricius, 1781.

Canaria Becker, Ann. Mus. Zool. Acad. Sci. Imp. St. Pétersbourg, vol. 17, p. 462, 1913a. Type of subgenus: *Anthrax brunneipennis* Macquart, 1838, by original designation. Preoccupied by Partington (1835), also others.

Canariellum Strand, Arch. Naturgesch., vol. 92, Abt. A., pt. 8, p. 48, 1928. Change of name.

Bezzi (1924), pp. 142-143, key to 17 Ethiopian species.

Paramonov (1924, 1925, 1926), keys and descriptions to many Palaearctic species.

Séguy (1926), p. 213, key to 3 species from France.

Engel (1934), pp. 363-368, keys to 17 species.

Austen (1937), pp. 95-96, key to 9 species from Palestine.

Hesse (1956), pp. 149-181, keys to 90 Ethiopian species.

Rather large flies of characteristic form and appearance. They are shining black, or brownish-black flies with the abdomen broad, slightly oval, sometimes a little wider than the thorax even in males, the surface only a little convex so that they appear to be somewhat flattened. Palaearctic species have conspicuous, narrow or wide, postmarginal, pale yellow or orange fascia on the tergites, first tergite sometimes excepted, and these fasciae may be separated in the middle so that there is a series of lateral bandlike spots instead of continuous fascia. The numerous South African species lack these yellow bands, the abdomen being wholly black or nearly black. The wing of Palaearctic species shows a characteristic, diffusely edged, brown band of infuscation covering the costal, first basal, sometimes the second basal cell, base of marginal cell and in various species extending to, beyond, or just before the origin of the second submarginal cell or downward as a crossband over the

whole end of the discal cell; South African species besides having similar patterns often have the wings spotted.

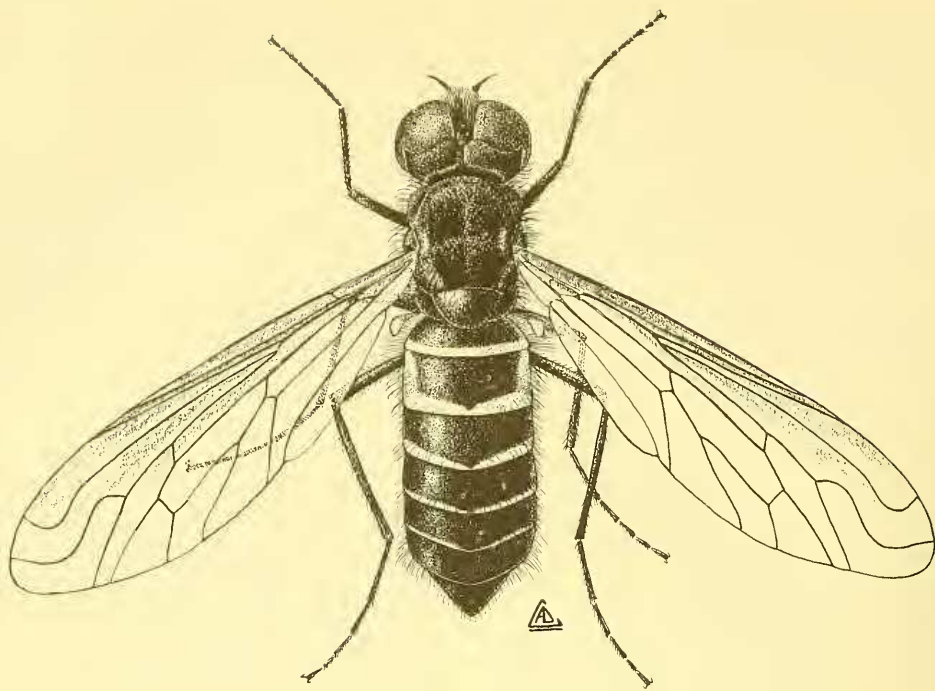
The wing shows only 2 submarginal cells with the marginal cell wide apically, recurrent at apex, sometimes a little swollen but never conspicuously swollen. The first posterior cell and the anal cell are always open.

The head is hemiglobular, the short, robust proboscis barely extends beyond the confines of the oragenal recess. Front and face are short, the latter receding. The first antennal segment is large, flattened above, swollen toward the apex so that the beadlike second segment and the bulbous, apically attenuate third segments are strongly divergent. Occiput strongly indented near midpoint of eye margin. Upper occiput extensive, the lobes touching. The lower occiput is generally about half as long as the upper occiput. Pile of thorax and abdomen abundant, long, coarse, erect or semierect, forming shaggy tufts alongside of abdomen which, however, are not flattened as is so characteristic of certain other genera.

I agree with Hesse (1956) that *Lomatia* Meigen represents a highly plastic genus. The genus as represented in South Africa is certainly dissimilar to the representatives in Europe. Probably *Lomatia* Meigen is a recent genus or one that is now reaching a peak of speciation; what little we know of life histories (European) indicates predation on grasshopper eggs. Certainly there are enough species of locusts in South Africa and enough varied ecological situations to provide for an explosion of species.

Lomatia Meigen is a genus characteristic of and confined to the southern half of the Palaearctic, especially the Mediterranean, North Africa, Asia Minor, and extending below the Sahara into South Africa where Hesse (1956) lists 87 species in his remarkable memoir.

Apparently, there are a few Australian flies near *Lomatia* Meigen, and I place them here provisionally. I have collected some in Australia myself, but I have

TEXT-FIGURE 44.—Habitus, *Lomatia lateralis* Meigen.

no males. It is probable that these are distinct from their European relatives, but a decision must depend upon the comparison of male genitalia.

The African species of *Lomatia* Meigen, as Bezzi (1924) notes, are quite dissimilar from the Palaearctic species in a number of ways. Generally speaking, the discal cell in the African species ends acutely; this is almost the rule, but there are a few exceptions such as *uniplaga* Hesse and *pterosticha* Hesse; moreover, where the European species are polished black with divided fasciae of pale yellow or at least medially narrowed bands upon the tergites, the African species are dull black without yellow bands; the tergites posteriorly have bands of appressed, curled, glittering, often golden hair; in some, the wings are mottled with obscure spots. It should be noted further that while the posterior margin of the eye is typically deeply indented in the middle, I have one South African species with completely hyaline wings and almost no indentation upon the posterior eye margin.

Included in *Lomatia* Meigen, I place *Canariellum* Strand as a subgenus.

Canariellum Strand, with type of subgenus *Anthrax brunnipennis* Macquart (1838) was described from the

Canary Islands by Becker (1913a) under the name *Canaria* Becker. I am unable to pass upon the validity by which Strand changed the name. Frey illustrated this fly by a photograph in one of his papers. It may be recognized by the unusually long, very dark wings, and the antenna; third segment small, base small and bulbous, style long and quite slender; first segment strongly rounded.

Length: The flies in the genus *Lomatia* Meigen vary greatly in size. Body length: 5.5 to 16.5 mm. Wing length: 5.5 to 19.5 mm. Many of the South African species are rather small, 6 to 7 mm. in length; some species vary much in size; other species are characteristically large flies, such as the European *superba* Loew and the South African *longitudinalis* Loew, besides still other species.

Head, lateral aspect: The head is subglobular, conspicuously convex on the anterior half and equally so above and below the antennae. The occiput is very prominent above both in males and females; in females it is sometimes more than twice as extensive behind the vertex as it is at the lower eye corners, and the posterior eye margin is deeply and triangularly or sometimes roundly indented in the middle, but never with bisect-

ing line. Pile of the occiput sparse, short, rather bristly, somewhat appressed or directed forward toward the eye margin; in some species it is much more dense, and always with a dense fringe of short, erect pile along the inner margin of the large, deep, central, occipital cup. The front is convex, a little swollen. The front has dense, shaggy, coarse or bristly pile over the entire front and vertex, except upon a small medial triangular space immediately in front of the antennae, which is pollinose only, or sometimes only shining and marked by a characteristic V-shaped depression or pit. The ocellar tubercle is prominent with pile similar to that of the front, the ocelli set in an isosceles triangle.

Below the antennae the face is short, extending no further than the front above the antennae, the oragenal cup is also short and extends to the base of the antennae. The lateral face and gena are pollinose and bear dense, rather long, shaggy or bristly pile, extending down to the base of the proboscis. The proboscis is short and stout with short, fleshy, muscoidlike, rugose labellum, which occasionally is long and pointed as in *Lomatia infuscata* Bezzi. The proboscis is thrust forward or somewhat upward, and in some species it is no longer than the oral recess, in others it may extend a little beyond, and in a few species it is long. The palpus is elongate, slender, clavate and consists of only one segment; it is sometimes almost bare, with only minute pubescence; in others it bears long, shaggy pile laterally near the apex.

The antennae are attached at the middle of the head; the whole antennae are relatively small. The first segment is large, swollen medioapically, generally longer than the second segment. The first segment has short, setate pile in the middle dorsally. It also has conspicuous, long, brushlike tufts of rather bristly pile, which are long laterally and below and equal in length to the thickness of the segment but with shorter, medial pile where the segments converge. The small, beadlike second segment is firmly attached at the outer lateral margin of the first segment, hence this segment and the third segment are strongly divergent. The third segment is either pyriform at the base and usually drawn out into strongly attenuate, stylelike lobe bearing a bristle at the apex. The swollen, bulblike base is as wide or sometimes less wide than the second segment, and the swollen part is approximately as long as wide before narrowing abruptly into the apical process. The apical process, when viewed from the inner side, is strongly asymmetrical and arises from one edge of the third segment; again, in a few species, as in *Lomatia acutangula* Loew, the whole third segment is very gently and gradually tapered to the apex, which usually bears a small spine or minute microsegment.

Head, anterior aspect: The head is more narrow than the thorax. The eyes in the male always separated, though sometimes very narrowly by as little as the width of one ocellus as in the type-species, or sometimes by as much as the width of the ocellar tubercle. The eyes of the female are separated by less than or a little

more than twice the space between the outer margins of the posterior ocelli and occasionally 3, or more than 3, times this distance. The oragenal cavity is obliquely directed upward and is comparatively deep with the inner walls vertical, or even overhanging at the bottom of the head. Near the middle the oragenal recess is pinched-in somewhat toward the middle and is triangular above, leaving a bare, longitudinal ridge extending to the base of the antennae. The width of the facial space is about equal to the width of the eye, but widens a little above toward the antennae. The facial part of the oral recess and the deeply sunken border of the narrow genal portion all bear dense, rather long pile. Tentorial fissure quite deep. The posterior part of the buccal excavation may descend well below the eye and back beyond the posterior eye corners. From the posterior aspect the strongly lobed occiput has a very narrow fissure above, the two lobes usually touching.

Thorax: The thorax is short and compact, widest posteriorly across the postalar callosity. The mesonotum is not longer than wide; it is comparatively low; slightly more raised anteriorly. It tends to be somewhat flattened in the middle and behind. The color of the entire thorax is black, polished and shining on the mesonotum and scutellum but sometimes becoming reddish brown on the lower part of the pleuron. Pile of the mesonotum dense, fine, erect and moderately long, nowhere obscuring the ground color. It is equally long on the humeri, rather stiff between them, with pile extended continuously over the notopleuron. There are several weak, notopleural bristles that do not rise above the pile. Considerable dimorphism may be seen in the females of some species with respect to the pile. In males the thoracic pile is entirely black, except that of the squama, but in females the mesonotal, upper mesopleural, and scutellar pile is golden, the remaining pleural pile and squamal pile white.

Postalar callosity with 2 or 3 weak bristles. Scutellar disc with a few long, fine, erect, scattered hairs, and the margin with similar long hairs scarcely or not at all stouter. Scutellum rather large, thinning toward the posterior margin. The pleuron is pollinose. Almost the whole of the mesopleuron bears bushy, long, coarse pile along the upper border that is directed upward. On the lower half the pile is finer, directed outward, or in females the pile is coarser and the pile is directed downward. Upper half of sternopleuron with fine, erect pile, or with subappressed tufts of bushy pile. Pteropleuron pollinose only. Hypopleuron bare, except for 1 or 2 hairs. Metanotum, however, with the characteristic, dense band of stiff pile. There is no hair in front of the posterior spiracle but behind the spiracle there is a conspicuous, large tuft of appressed, coarse pile. Squama peculiar in the presence of a very wide, broad, extensive band of long, plumelike pile. Propleuron with long, collarlike pile.

Legs: The legs are comparatively stout without being swollen, the anterior femur may be slightly en-

larged toward the base. All of the femora bear appressed, small scales, somewhat larger and longer dorsally on the hind femur. Anterior femur with a few fine, bristly or stiffened hairs ventrally of no great length. Middle femur similar with a few slender bristles anteroventrally near the apex. Hind femur with 3 or 4 rather stouter bristles anteroventrally on the outer half, sometimes as many as 7 or 8. Anterior tibia slender with 12 tiny, short, oblique, spiculate hairs dorsally, a few others posteriorly. Middle tibia with longer, oblique, slender bristles in 4 rows. There are 10 anterodorsally, the same number posterodorsally, and about the same number on each side ventrally. Hind tibia with 10 or 12 dorsal bristles, 7 or 8 anteroventral bristles, 6 or 8 much more slender posteroventral bristles but only minute, erect setae dorsomedially. All of the tibiae are progressively longer, the hind pair being the longest. All tarsi short, claws slender, rather strongly but gradually curved on the apical half, the pulvilli long and slender.

Wings: The wings are elongate, narrowing a little toward the base, and characteristically tinged with light reddish sepia brown to a varying extent but generally extending over the whole anterior border to a little beyond the anterior crossvein. This somewhat diffuse brownish color includes the whole of the first basal cell, anterior border of the discal cell, and sometimes extends diffusely along the posterior border of the second basal cell. In some species the whole wing is somewhat lighter on the basal part and the ground color tends to extend somewhat as a crossband over the whole outer half of the discal cell and a little below it. In several South African species the wings bear distinct but somewhat diffuse spots subapically over the base of the second submarginal cell, end of the discal cell and beyond it, base of the third posterior cell, end of second basal cell and base of discal cell. In *Lomatia neavei* Bezzi the entire wing is blackish except the costal cell and the posterior basal angle, a few individuals showing a hyaline streak in the center of the discoidal cell and in the posterior cell. There are only 2 submarginal cells and there is a characteristic form to the end of the marginal cell and the submarginal cell. Marginal cell slightly widened apically but forming a rounded never accentuated bulge. The second vein returns to the costa either rectangularly or slightly recurrent. The anterior branch of the third vein rises abruptly, makes a rounded bend and then turns up strongly toward the costa so that the first marginal cell, which is of nearly equal width throughout, makes a rather strong upward bend to the foremargin of the wing.

There are 4 posterior cells, all open, the first posterior cell always open though sometimes a little narrowed. Anal cell widely open, the anal vein straight for most of its distance, but curved apically. The anterior crossvein is oblique and enters the discal cell at the outer fifth of the type-species and sometimes either a little before or a little beyond the outer fifth. The axillary lobe is long

and slender, equally narrowed basally and distally. The alula is quite narrow and linear with a plane margin. Ambient vein complete.

Abdomen: The abdomen is broadly oval, as wide basally as on the thorax and in both males and females wide apically. The whole abdomen is only very gently and slightly convex. In African species the abdomen is entirely black. In the type-species and in Palaearctic species the abdomen is characteristically marked with narrow or wide posterior yellow margins on the tergites, sometimes broken into pairs of fasciate or triangular spots by these bands being interrupted in the middle, as in *Lomatia suberba* Loew. The pile of the abdomen is rather long and fine and erect on the first 4 tergites, very dense laterally on the first tergite but becoming rather curled and appressed on the last 4 tergites. Also, the lateral pile of the tergites is more dense, stiff and bushy but never with long, flattened tufts as in some related genera. On the abdomen of males the pile on the first segment is rather whitish and straw colored, but golden yellow in the females. The marginal pile of the tergites in the males is black but in the females yellowish white. I find 9 tergites in the males, the last one small and overhanging the genitalia. In females I find only 7 tergites, the seventh tergite and sternite each bearing a dense fringe of curled pile surrounding the apex of the female abdomen.

Dr. A. J. Hesse was able to study a very large assemblage of species in this genus; for this reason I quote his comments on the male genitalia:

Hypopygium of males usually reversed in position, the true dorsal side being directed to the sides or more frequently to the ventral side, and its opposing sternite (last unmodified sternite) dorsal in position; neck region of the two symmetrical basal parts more or less narrowed and covered with hairs which are sometimes dense, longish, conspicuous and situated in distinct punctures; outer apical angle of each basal part sometimes angularly, or even sharply, produced; beaked apical joints remarkably uniform in shape, ending in a slightly outwardly and downwardly directed pointed beak and usually covered with fine shortish hairs; aedeagus shaped; lateral struts from middle part very uniform in shape, but sometimes tending to be broadish or narrowed apically or even narrow and rod-like; basal strut variable in shape, very frequently with its dorsal edge incised or emarginate or sharply pointed and in many forms with a distinct flattened, ledge-like, triangular extension on each side basally.

From my own study, I find the male terminalia from dorsal aspect, epandrium removed, show a long slender body with peculiar dististyli, which have a large, wide, curved tubercle. In lateral aspect it has a noselike tubercle at the apex in the type-species. The epiphallus is quite long, and relatively slender. From the lateral aspect the basistylus is long, a little thicker though widened basally and the epiphallus and ejaculatory process are long and spoutlike. Epandrium quite large and rhomboidal in shape. Cerci large. Basal apodeme small.

Material available for study: I have representatives of European species presented to me by the Museum of Comparative Zoology and by Professor J. Timon-

David of Marseille. Also, material of South African species received through the courtesy of Mr. B. R. Stuckenberg of the Natal Museum.

Immature stages: One species has been associated in the larval state with the egg pods of locusts. See discussion under life histories.

Ecology and behavior of adults: Hesse (1956) records one species taken on the flower clusters of *Bezelia*.

Distribution: Neotropical: *Lomatia caloptera* Macquart, 1834 (probably belongs in another genus).

Palaeartic: *Lomatia abbreviata* Villeneuve, 1912; *alecto* Loew, 1846; *armeniaca* Paramonov, 1924; *bella* Loew, 1873; *bella tibialis* Loew, 1873; *belzebul* (Fabricius), 1794 (as *Anthrax*), *belzebul lowei* Paramonov, 1931; *brunnipennis* (Macquart in Webb), 1838 (as *Anthrax*); *comata* Austen, 1937; *conspicabilis* Austen, 1937; *erinnis* Loew, 1869, *erinnis erinoides* Paramonov, 1928, *erinnis obscuripennis* Loew, 1869; *fasciculata* Loew, 1869; *fuscipennis* Portschinsky, 1887; *gracca* Paramonov, 1928, *gracca erinoides* Paramonov, 1931; *grajugena* Loew, 1869; *gratiosa* Loew, 1869; *hamata* Austen, 1937; *hamifera* Becker, 1915; *hecate* Meigen, 1839; *infernalis* Schiner, 1868 [= *infernalis* Loew, 1869, = *tisiphone* Lowe, 1869]; *innominata* Austen, 1937; *lachesis* Egger, 1859, *lachesis gracca* Paramonov, 1928 [= *limbata* (Megerle in litt. in Meigen), 1820 (as *Stygia*), = *tisiphone* (Loew in litt. in Schiner), 1862]; *lateralis* (Meigen), 1820 (as *Stygia*), *lateralis atropos* Egger, 1859 [= *belzebul* (Panzer), 1797 (as *Anthrax*)]; *lepada* Austen, 1937; *montana* Paramonov, 1924; *multifasciata* Austen, 1937; *pallida* Tsacas, 1962; *persica* Paramonov, 1924; *polyzona* Loew, 1869, *polyzona meridiana* Paramonov, 1931 [= *hecate* Loew, 1846 (not Meigen), = *polygona* Bezzi, 1903, lapsus]; *rogenhoferi* Nowicki, 1867, *rogenhoferi caspica* Paramonov, 1926; *rufa* Wiedemann, 1818; *sabaea* (Fabricius), 1781 (as *Bibio*); *shelkornikovi* Paramonov, 1924; *superba* Loew, 1868; *taurica* Paramonov, 1925, *taurica completa* Paramonov, 1925; *variegata* Paramonov, 1925.

Ethiopian: *Lomatia acutangula* Loew, 1860, *acutangula transvaalensis* Hesse, 1956; *albata* Hesse, 1936; *albicincta* Hesse, 1956; *albicoma* Hesse, 1956; *albizonata* Hesse, 1956; *albulata* Hesse, 1956; *apicalis* Hesse, 1956; *arenaria* Hesse, 1956; *asaphoedema* Hesse, 1956; *atrella* Hesse, 1956; *basutoensis* Hesse, 1956; *bembesiana* Hesse, 1956; *berzeliaphila* Hesse, 1956; *bevisii* Hesse, 1956; *brunnitincta* Hesse, 1956; *canescens* Hesse, 1956; *chracopectera* Hesse, 1956; *cinerea* Loew, 1869; *citraria* Hesse, 1956; *cognata* (Walker), 1849 (as *Anthrax*); *composoma* Hesse, 1956; *conicera* Hesse, 1956; *conocephala* (Macquart), 1840 (as *Anthrax*); *consors* Hesse, 1956; *conostoma* Hesse, 1956; *crossodesma* Hesse, 1956; *desmophora* Hesse, 1956; *dimidiata* Hesse, 1956; *eremia* Hesse, 1956; *fasciolaris* Walker, 1857; *flavifrons* Hesse, 1956; *fucatiipennis* Hesse, 1956; *fulva* Hesse, 1956; *fulvipleura* Hesse, 1956; *gigantea* Bezzi, 1912; *glaucciella* Hesse, 1956; *grahami* Hesse, 1956; *grisealis* Hesse, 1956; *halteralis* Hesse, 1958; *hemichroa*

Hesse, 1956; *heterocoma* Hesse, 1956; *hylesia* Hesse, 1956; *infusata* Bezzi, 1921; *inornata* Loew, 1854; *jansei* Hesse, 1956; *kalaharica* Hesse, 1956; *koakoana* Hesse, 1956; *latifrons* Hesse, 1956; *latiuscula* Loew, 1860; *lawrencei* Hesse, 1956; *leucochlaena* Hesse, 1956; *leucophasia* Hesse, 1956; *leucopsis* Hesse, 1956; *liturata* Loew, 1860; *loewi* Bezzi, 1912 [= *inornata* Loew, 1860 (not Loew, 1854)]; *longitudinalis* Loew, 1860; *marleyi* Hesse, 1956; *matabeleensis* Hesse, 1956; *melampogon* Loew, 1860; *melanoloma* Hesse, 1956; *melanthia* Hesse, 1956; *mesoleuca* Hesse, 1956; *mitis* Lowe, 1860; *mollivestis* Hesse, 1956; *monticola* Hesse, 1956; *mozambica* Hesse, 1956; *natalicola* Hesse, 1956; *namaqua* Hesse, 1956; *neavei* Bezzi, 1924; *nigrescens* Richardo, 1901, *nigrescens aterrima* Hesse, 1956, *nigrescens bulawayoensis* Hesse, 1956; *nivosa* Hesse, 1956; *oreoica* Hesse, 1956; *orephila* Hesse, 1956; *ovamboensis* Hesse, 1956; *pedunculata* Hesse, 1956; *phaenostigma* Hesse, 1956; *pictipennis* (Wiedemann) 1828 (as *Anthrax*) [= *aurata* (Macquart), 1846 (as *Anthrax*), = *centralis* (Macquart), 1840 (as *Anisotamia*)]; *plocamoleuca* Hesse, 1956; *pseudofasciata* Hesse, 1956; *pterosticta* Hesse, 1956; *pulchriceps* Loew, 1860, *pulchriceps linganaui* Hesse, 1956, *pulchriceps ogilviei* Hesse, 1956, *pulchriceps tinctella* Hesse, 1956; *punctifrons* Bezzi, 1924; *purpuripennis* Hesse, 1958; *salticola* Hesse, 1956; *semiclara* Hesse, 1956; *sepioptera* Hesse, 1956; *sericosoma* Hesse, 1956; *simplex* (Wiedemann), 1819 (as *Anthrax*); *sinuosa* Hesse, 1956; *spiloptera* Bezzi, 1924; *stenometopa* Hesse, 1956; *stenoptera* Hesse, 1956; *subcaliga* Hesse, 1956 *tenera* Loew, 1860; *thysanomela* Hesse, 1956; *uniplaga* Hesse, 1956; *vicinialis* Hesse, 1956.

Oriental: *Lomatia brunnipennis* (Wulp), 1868 (as *Comptosia*).

Australian: *Lomatia anthracina* (Thomson), 1869 (as *Comptosia*); *australensis* Schiner, 1868; *sorbicula* (Walker), 1857 (as *Anthrax*), *sorbicula*, erratum.

Genus *Anisotamia* Macquart

Anisotamia Macquart, Diptères exotiques, vol. 2, pt. 1, p. 81, 1840. Type of genus: *Anisotamia ruficornis* Macquart, 1840. Designated by Coquillett, p. 507, 1910a, the first of 2 species. The second species has been transferred to *Lomatia* Meigen.

Since I have not seen *Anisotamia* Macquart, I give a translation of Engel who describes this genus as follows:

In its plastic characteristics this genus scarcely differs at all from *Lomatia* Meigen, from which it is distinguished only by the closed first posterior cell, the prevalence of yellow body coloration, and its size.

The eyes of the male are separated by the ocellar tubercle and diverge immediately below it; in the female the vertex of the head is somewhat broader. The frons is thickly pilose almost up to the ocellar tubercle, and with hairs of the same length as the face. The thorax has some yellow parts in basic color too. The pile on the metapleuron is wanting or absent, as in the case of *Lomatia* Meigen, but the sides of the metanotum are similarly pilose. On the yellow legs, the pulvilli are fairly narrow. The

abdomen is the same width as the thorax, and is about one and a half times as long, primarily yellow in its basic color, with black anterior parts on the tergites and sternites. The epipygium is small, and like the probably spined ovipositor, concealed in the last segment.

Metamorphosis unknown.

The only species is spread over all of north Africa as far as Asia. The genus *Oncodocera* Macquart, cited in the Kertész catalogue as a questionable synonym for *Anisotamia* Macquart, is a distinct genus with a completely different body and antenna.

Only a single species is known. Engel describes the unique type-species in the following terms:

Male and female in large part predominantly straw yellow. The head is straw yellow pilose on a reddish yellow basal color of face and front; the back of the head is black, but also with short yellow hairs. The antennae are reddish yellow, of the same form as in *Lomatia* Meigen; a few short little bristles on its basal segments are black. The eyes of the male are separated from each other by the ocellar tubercle, and closer to each other for only a short distance before it; in the female, on either side next to the ocellar tubercle, there is an intermediate space, which is not quite as long as the distance of the front one from the side ocellus, and the area around the ocellar tubercle is red yellow in base color. The facets are slightly enlarged in the male in a band or area next to the front. The thorax is black in basic color, somewhat shiny on the mesonotum, dull on the pleuron; the base of the yellow scutellum is also more or less black. In the female the sides of the mesonotum at the level of the alar callosity are also red yellow in basic color. The pile of the prosternum, pleura and coxa is yellowish white; that of the notopleural suture, of mesonotum and scutellum is straw yellow. The legs are yellow with short, black little bristles and darkened tarsi. The pulvilli are short and narrow. The wings weakly gray yellow, with yellow-brown bordered veins, of which only the tips of the second and third radius and the forked branches of the fourth and fifth and the anal vein are un-darkened.

The venation corresponds to that of *Lomatia* Meigen, only the first posterior cell is closed off and stalked. The discal cell is shorter and wider than in *Lomatia* Meigen; the diagonally situated anterior crossvein, however, is in the same position as in the latter. The wings of the female are colored somewhat paler. Squama with white fringe; haltere ochre yellow. On the abdomen the sides of the first tergite are protruding and bear longer straw yellow hairs than the others. The anterior margins of all tergites are black on half their segment length, which color extends with an arc in the middle, into the reddish yellow back half. In other words, the back edges of the tergite are very broad, those of the sternite also broad and colored yellow. On the latter, only the front edge remains dull black for a third of the length of the sternite. The pile of the abdomen is also straw yellow.

Material available for study: There is a single female individual of *A. ruficornis* Macquart in the collections of the British Museum (Natural History), which was recorded from Palestine by Austen (1937).

Since *Anisotamia* Macquart is so much like *Lomatia* Meigen in every respect, except for the closed first posterior cell, I have not redescribed it; instead I quote Engel's description.

Immature stages: Unknown.

Ecology and behavior of adults: Austen recorded the above-mentioned female as apparently investigating and possibly ovipositing in the nest of fossorial Hymenoptera. The species is well known in Egypt.

Distribution: Palaearctic: *Anisotamia ruficornis* Macquart, 1840.

Genus *Ogcodocera* Macquart

FIGURES 122, 713, 724, 911, 912

Ogcodocera Macquart, *Diptères exotiques*, vol. 2, pt. 1, p. 83,

1840. Type of genus: *Mulio leucoprocta* Wiedemann, 1828, by monotypy, as *Ogcodocera dimidiata* Macquart, 1840.

Oncodocera Osten Sacken, *Bull. U.S. Geol. Surv.*, vol. 3, p. 247, 1877, emendation.

Small flies of black color and broad, rather flattened abdomen. They can be quickly recognized by this broad, rather flattened, short oval abdomen, which is quite wide apically in males, with the last tergite an equilateral triangle in females, but more especially by the peculiar distribution of pile. The surface of the tergites has fine, scattered, long, erect hairs, but the sides of the tergites have a dense flat brush of matted hair extending in a flat platelike formation out directly away from the sides; this lateral hair band is very long and at least half as long as each lateral half of the tergites. Lateral pile in the type-species is entirely brownish black, but the posterior margin of the last tergite has an equally long fringe of opaque snow-white pile forming a shelf above the small genitalia.

Wings with basal half obliquely brownish, the outer part hyaline. There are 2 submarginal cells, the anterior branch of the third vein is gently sinuous and the marginal cell is scarcely widened apically. Four posterior cells are present, all of them open widely; the anal cell is closed in the margin or near it. The anterior crossvein enters the discal cell at or a little beyond the outer third of that cell.

The head is hemiglobular, but the occiput is longer in females and at least twice as long as in males. The upper occipital lobes are tightly apposed, and the indentation near the midpoint of the posterior eye margin is comparatively deep. The antennae are small and set at or slightly below the middle of the head so that the front, while very short in extension, is of great length from vertex to antenna and strongly convex. The first antennal segment is relatively large, widened apically, the second segment small, the third elongate conical and strongly tapered to a fine point and bearing a minute apical spine.

Ogcodocera Macquart is certainly related to *Lomatia* Meigen, an Old World genus. It differs in the smaller size, the closed anal cell, widely open in *Lomatia* Meigen, and in the exceptionally wide flattened bands of long pile along the sides of the abdominal tergites. *Ogcodocera* Macquart is a genus of few species restricted to the Nearctic and Neotropical regions.

Length: 5.5 to 8 mm.; wing, 6 to 9 mm.

Head, lateral aspect: The head is comparatively short with the upper anterior half very convex and the lower anterior half below the antennae more nearly plane due to the receding face and the receding eye. The occiput is very extensive on the dorsal half, even more so in the middle, at which point the posterior eye margin is angularly indented and has a small notch. The upper

eye facets are considerably enlarged. The pile of the occiput is dense but quite short and appressed forward and reaches the eye margin. There is a fringe of short erect hairs along the inner margin of the circular occipital cup. The front is convex, densely covered with long pile, erect along the eye margins, somewhat appressed in the middle of the front. This pile is scaly, silvery, and matted in the males of some species, black and erect in other species; this pile continues to extend down between the widely separated antennae. The face is very short, the oragenal recess lying below the eye margin. The eye is extensive, somewhat reniform.

The proboscis is short, flattened laterally with a short, flattened, lanceolate labellum turned upward. The proboscis is slightly longer than the oragenal recess. The palpus is quite slender and composed of one segment and about one-third as long as the proboscis. It bears a very few fine, long, appressed hairs. The antennae are small, the first segment short, broad, almost completely concealed by the matted pile of the front overlapping its own extensive pile. The first segment bears a tuft of long, silvery, flattened hairs above, another below and medially with rather less pile laterally. The second segment is only about half as long as wide, the third segment is a little longer than the first 2 segments combined. It is long conical being gradually tapered from the base and has a minute spine at the apex. At the base it is not quite as wide as the second segment.

Head, anterior aspect: The head is circular, and not quite as wide as the thorax. At first sight it appears to be much more narrow than the thorax due to the deceptive, long, bushy pile on the mesonotum and pleuron of the thorax. Eyes in the male holoptic, in contact for about one-fourth of the distance from ocellus to antennae. The ocellar tubercle is small but high and the ocelli are set in a short isosceles triangle. A tuft of fine, stiff hairs arise between the ocelli. The front is quite wide forming an almost equilateral triangle. In females the eyes are separated a space equal to the first two antennal segments. The small, low ocellar tubercle lies at the posterior corner of the eye and is not set slightly forward as in the male. The anterior part of the vertex is swollen, but the front is rather sunken actually below the level of the eye; its pile is similar to that of the male but less extensive. Most of the antennal pile is brownish or black. The oragenal cup is elongate, rather deep, the inner wall vertical or even partly cupped over; near the middle it is somewhat compressed inward, and it is separated from the eye margins by a deep foveal recess. This shelving outer wall bears a fringe of coarse, erect pile of no great length. From the posterior aspect the occiput is bilobate with the dorsomedial fissure and accompanying depression extending only half the length of the occiput. The occipital lobes are tightly apposed.

Thorax: The thorax is quite short but distinctly widened posteriorly; the mesonotum rather flat and low. The whole thorax is of very little depth. The pile of the mesonotum is dense, erect, fine and quite bushy

and rather long. In the material that I have seen, these flies are usually more or less denuded on the posterior half of the mesonotum, scutellum, and generally rather widely over the middles of the tergites. However, it appears that normally this fine, long, erect pile is comparatively abundant over the whole of the mesonotum and the tergum of the abdomen and much of the disc of the scutellum, but certainly this pile is much more dense and bushy on the anterior third of the mesonotum, the humerus and the notopleuron, and perhaps even longer and denser on the upper mesopleuron. There are fewer hairs on the lower mesopleuron and sternopleuron; the pteropleuron is without pile, but there is long, dense pile on the metanotum, and a large, oval, conspicuous tuft of long pile on the metapleuron in front of the halteres, a smaller, shorter tuft behind. The scutellum is rather large, wide, slightly triangular but obtuse and rather flattened. The squama is small and quite short but bears a peculiar, very wide, dense brush of pile widened out dorsoventrally. In this respect it is quite like *Lomatia* Meigen. In *Ogcodocera* Macquart there is a sexual dimorphism in the color of the pile. In females the mesopleural, squamal, scutellar and basi-abdominal pile, including the lateral tufts, is snow white. In males these areas have reddish or brownish-black pile.

Legs: The legs are weak; the femora are slender and loosely covered with flat-appressed, rather long, dark scales. The small anterior femur is shorter than the middle pair and has only a few fine hairs below, some 8 or 9 altogether. The middle femur is considerably shorter than the hind femur, and contains 15 or 20 long, fine, ventral hairs. Hind femur with a similar number of hairs below and 2 or 3 quite slender, apical, bristly hairs ventrally, a few others dorsally. Middle tibia similar, the stiff dorsal hairs a little longer; the 7 or 8 oblique, short, bristly hairs ventral in position. Hind femur with 8 or 9 very slender, short bristles antero-ventrally and with 10 to 12 bristles anterodorsally, and nearly as many dorsomedially. There are 6 ventro-medially. Tarsi short and slender, claws long and straight but sharply curved at the apex; the slender pulvilli are long.

Wings: The wings are rather broad basally with the basal half obliquely dark reddish sepia but scarcely extending into the axillary lobe and not all of the anal cell. The alula and base of the axillary lobe, however, are dark. The sepia color fills out the costal cell and extends farther back basally in the marginal cell, still farther back in the first submarginal cell and colors the base of the discal cell and extends downward posteriorly along from the base of the fourth posterior cell. The remainder of the wing is hyaline and villose. There are 2 submarginal cells with the anterior branch of the third vein arising obliquely and rather sigmoid. Marginal cell is not at all widened apically. All the posterior cells are widely open and the anal cell is closed in the margin, or more usually has a short stalk. Ambient vein complete, the alula moderately wide.

Abdomen: The abdomen is quite broadly oval, usually wider than the thorax and rather strongly flattened so that it is only a little convex. I find 7 tergites in the male and 7 in the female. Unabraded, fresh material has a considerable amount of long, fine, erect pile on the middle of the tergites with some shorter, flat appressed, fine, nonscaliform pile arising at the base of the tergites and posteriorly directed and appressed on the tergites. The abdomen, however, is conspicuous and noteworthy for the extraordinarily long fringes arranged along the sides of the tergites as a flat bank of outwardly directed, overlapping tufts of pile. In length these tufts of pile are almost as long as half the width of the abdomen; hence they add materially to the apparent width of the abdomen. Female terminalia are surrounded and concealed on each side by a dense, matted tuft of pile leaving the barest longitudinal slit visible. Male terminalia small, the basimeres and dististyli turned ventralward side by side beneath a curiously notched and hoodlike, apical tergite.

The male terminalia from dorsal aspect, epandrium removed, show an unusually slender body with a very long, epiphallus progressively widened toward the base. The dististyli are unusually large and viewed from above are stout, obtuse, long, wide, and conspicuous. Viewed laterally, however, they are even more conspicuous, and strongly curled upward. The basistylus is long, but slender, the basal apodeme, small and short, the epiphallus is long and spoutlike but curved upward on the outer part. The epandrium is small, triangular, with a very long basiventral lobe or process.

Material available for study: I have collected 2 species in this small genus: one Nearctic species, not common in Mississippi; another species in southern Mexico. I have a third species from south Brazil.

Immature stages: Unknown.

Ecology of adults: These flies can be collected on flowers such as fleabane and other composites in early summer.

Distribution: Nearctic: *Ogcodocera analis* (Williston), 1901 (as *Oncodocera*); *leucoprocta* (Wiedemann), 1828 (as *Mulio*) [= *dimidiata* Macquart, 1840, = *leucotelus* (Walker), 1852 (as *Anthrax*), = *terminalis* (Wiedemann), 1830 (as *Anthrax*)].

Bryodemina Hull, new genus

FIGURES 207, 375, 695, 898, 899

Bryodemina Hull, Ent. News, vol. 77, p. 227, 1966, preoccupied Fieber, 1853. Type of genus: *Anthrax valida* Wiedemann, 1830.

Brachydemina, new subgenus. Type of subgenus: *latisoma*, new species.

Very large, giant flies of exceptionally stout, robust form. The are related to *Ogcodocera* Macquart, which are very much smaller, with flattened abdomen accentuated by the remarkably long, flattened tufts of pile along the sides of the tergites, which are scarcely notice-

able in *Bryodemina* Hull. In *Bryodemina* the first posterior cell is closed and stalked, the anterior crossvein, which is quite oblique, enters the discal cell at the outer fifth of the discal cell, not near the middle of the cell. The marginal cell is widened apically and ends obtusely. The third antennal segment is long, and gradually attenuated, narrow, and spikelike.

Flies are abundant in central Mexico. They are nearly related to another broad, wide, somewhat similar fly from Brazil, which I place in the new subgenus *Brachydemina*. Here the anterior crossvein is in the same relative position, very oblique, and the first posterior cell is greatly narrowed. The marginal cell is similar and the antennae are similar. Nevertheless, these very large flies have a thinned abdomen with very conspicuous radiating tufts of dense, flattened tufts of pile along the lateral margins of the tergites. Figured in Williston (1908).

Distribution: Central Mexico and southern Brazil.

Length: 22 mm.; rarely as little as 13 mm.; wing 17 to 20 mm.

I have before me 3 species of *Ogcodocera* Macquart, the type-species *leucoprocta* Wiedemann, *analis* Williston and a third species from South Brazil; all are almost equal in size, small, flattened, with lateral tufted pile and basally swollen third antennal segment. The anterior crossvein lies quite close to the middle of the discal cell, the first posterior cell is open maximally.

Elsewhere, I proposed the name *Bryodemina* for the giant bee flies with very robust, thickened bodies that formerly went under the name *Ogcodocera valida* Wiedemann. These differ from *Ogcodocera* Macquart, in the strict sense, of which I have 3 species before me, in the very thick body and giant size, in the closed and stalked, or narrowly open first posterior cell, and the position of the anterior crossvein, which is very strongly oblique and placed at the outer sixth of the discal cell. All of the 3 species of true *Ogcodocera* Macquart before me, including the type-species and one ranging to south Brazil, are of nearly uniform size, flattened body, basally swollen third antennal segment, the first posterior cell open maximally; the anterior crossvein is very near the middle of the discal cell and almost rectangular.

Head, lateral aspects: The head is subglobular and the occipital component is quite extensive with the dorsal lobes tightly apposed and with shallow crease. The posterior eye margin is only slightly indented and angularly indented with a very short bisecting notch. The lower half of the occiput is almost as strongly produced as the upper half; from the dorsal aspect it slopes strongly backward. The pile of the occiput is dense and fine, very short, and setate; the fringe around the occipital cup is quite short but dense and in the type-species pale in color in contrast to the black pile of the occiput. The face extends downward below the antenna a distance nearly equal the length of the first two antennal segments. In profile the extreme upper face and antennal base are scarcely visible and extend only a little

way beyond the eye. The prominent frontal area is somewhat convex and bulbose and is distinctly seen from the lateral aspect. On the lower part of the head, as well as the upper part above the antenna, the head is strongly rounded and retreating. Since the labellum of the proboscis extends above the apex of the oragenal recess and reaches the antennae, in consequence, this area rests against the antenna. This area is without pile. On each side, however, the pile is dense, coarse, directed outward, and extends a little beyond the second antennal segment. It becomes shorter below along the sides of the deep tentorial fissure; the lowermost sides of the gena and bottom of the head are without pile. The frontal area is opaque, and like all of the remainder of the head blackish, and the pile is dense, fine, erect, and nearly as long as the first two antennal segments.

The proboscis extends as far as the base of the antenna. The labellum is large, oval, flattened, and compressed on the outer half. It makes up not quite half the length of the proboscis. Palpus small, quite slender, deeply recessed, and lying against the base of the proboscis; it appears to have a minute, apical segment. The antennae are attached at the middle of the head; the first segment is quite large; swollen, twice as long and twice as wide as the small second segment; it bears some scattered, bristly pile laterally and also some medially toward the apex. The second segment is short, beadlike, with a row of stiff setae dorsally. Third segment at the base not quite as wide as the second segment and about twice as long as the first two segments together. It is gradually and distinctly but slightly tapered to the rather thick apex which bears a small, short spine; both upper and lower surfaces are nearly plane.

Head, anterior aspect: The head is nearly circular but much more narrow than the thorax. It is slightly flattened laterally and again at the vertex. The eyes in the male are strongly holoptic; they join at a point a little less than halfway from the posterior eye margin to the antennal base. The ocellar triangle is a short isosceles triangle and in the males makes up about one-half of the rather small vertical triangle. The ocellar triangle is quite low and scarcely visible in profile. The frons forms a widely expanding equilateral triangle, its length a little more than half the distance from the posterior eye margin to the antenna. In the female the occiput is even more extensive and may be approximately four-fifths as long as the eye itself; the junction point of the dorsal lobes in both sexes is set back a considerable distance from the corners of the eye and from it radiates slender grooves or striations. The oral opening is wider below, narrowing slightly above, and its walls are thin and knifelike on both sides.

Thorax: The thorax is quadrate and scarcely if any longer than the width across the postalar callosity; it is rather flat especially on the posterior half with the pile extraordinarily dense, black, fine, and erect, with a dark, reddish-brown cast, over the middle of the mesonotum when viewed laterally. The scutellum is quite large and hemispherical, slightly convex, but strongly

convex on the margin, and shining brown or blackish. The pile is dense, fine, erect, and blackish. Largely bare or denuded in the middle the pile is distinctly more abundant on the sides of the scutellum; this seems to be in part a continuation of the pile arrangement of the abdomen, which is much more dense on the sides of the abdomen leaving a narrow, longitudinal stretch down the middle which has only scanty pile. There are 4 or 5 quite slender bristles on the notopleural area which barely rise above the basic pile. There are several still more slender bristles on the postalar callosity. Pile on upper mesopleuron quite dense, fine and long, thinning out and becoming much more scanty below; it is still more scanty on the sternopleuron; the hypopleuron appears to lack pile. There are some scattered hairs on the pteropleuron, and much long fine pile is on the metanotum and also on the metapleuron above and in front of the spiracle. The haltere is small and slender; the squama has a very dense, long, fine fringe.

Legs: Rather small, and short on all 3 pairs. Femora stout without being swollen. Above, they bear coarse, appressed pile scarcely if at all flattened, and with short, fine, ventral fringe posteriorly on the first four femora. Each of these first four femora are slightly widened toward the base, and slightly bent at the apex; middle femur with 8 or 9 short, oblique, black bristles; hind femur with the appressed pile, black but shining and slightly flattened. The anteroventral margin bears 8 to 10 slender, oblique bristles and a few fine hairs. Anterior and middle tibiae quite slender, with short, fine, appressed setae and a few very fine, short, stiff, oblique bristlelike hairs dorsally. The hind tibia is at least twice as thick as the middle tibiae and very little longer; it is slightly compressed, and bears both dorsally. The hind tibia is at least twice as thick as the middle tibiae and very little longer; it is slightly compressed, and bears both dorsally and ventrally a dense, oblique fringe of moderately long, bristly hairs which lie in one plane and slightly longer dorsally and scarcely longer than the width of the tibiae. The fringe disappears toward the apex of the tibiae. Hind basitarsus narrow and tapered toward the apex and distinctly longer than the four remaining segments; pile short, fine oblique and setate. Pulvilli well developed; claws sharp; they are bent in a rectangular curve.

Wings: The wings are large, and narrow apically, quite wide basally. The axillary lobe is especially prominent. The alula has the postmargin plane or slightly concave and is about 3 times as long as wide; the ambient vein is continued strongly to the base of the alula. The basicosta is strongly widened and flattened in both sexes and bears dense, appressed, slightly flattened pile. I do not find any hook or spur. The veins are stout and the anterior crossvein is strongly oblique entering the discal cell at the outer sixth. The first posterior cell is closed and stalked; the two veins on the outer half of this cell are plane and the intercalary vein is long. The second vein makes a rectangular bend entering the costa at a right angle leaving the marginal cell widened and

obtuse at the apex. The anterior branch of the vein arises a gentle arch; it is bent before the middle; all the remainder is quite plane and it ends well before the apex of the wing. Anal cell closed with a short stalk; wing hyaline, with dark brown villi and with foreborder tinged with brown back as far as the discal cell and a little beyond the anterior crossvein.

Abdomen: Very large, thick and convex and wider than the thorax, appearing much wider because of the lateral mats of pile. There is much extreme, dense, long, fine, mostly shaggy and appressed pile over the tergites; this pile is a little more erect basally more matted and appressed posteriorly; it forms a wide, flaring, lateral mat. Narrowly, longitudinally the pile on the medial part of the tergites is thinned. The whole abdomen is faintly shiny black obscured by the dense pile. In type-species the lateral basal pile is black with the apical pile forming 2 widely separated expanding mats of brownish, cream-colored pile; in other species there is a transverse band of pile. Male terminalia small, posterior, recessed. There are 8 tergites visible above in males.

The male terminalia from dorsal aspect, epandrium removed, show a figure in general similar to that of *Ogcodocera* Macquart, to which it is related. The dististyli are wider apically, the lateral apodeme is longer and larger. The basal part of the aedeagus is much larger and bulblike. The epiphallus does not extend to the end of the basistylus. The epandrium is similar, but shorter and the cerci are larger.

Material available for study: A large series of both sexes of the type-species collected by the author and wife in central Mexico in the late summer of 1962. Some also collected by my son, Clovis Sillers Hull. Still others collected when in Mexico in 1951 a few miles from Cuernavaca. Two females of *Brachydemina* from Chapada, Brazil, presented to me through the courtesy of Dr. Curran.

Immature stages: Unknown.

Ecology and behavior of adults: The author found a series hovering in early afternoon beneath an apple tree on the outskirts of Cuernavaca; there was much high grass. Most of those collected in 1962 were in a lush meadow-like area about forty miles east of Guadalupe; others were in wet, dark woodland areas where there were patches of sunlight; a few were found on comparatively open hilly slopes. All were hovering and none were seen alight.

Distribution: Neotropical: *Bryodemina fasciata* (Williston), 1901 (as *Oncodocera*); *hedicki* (Paramonov), 1930 (as *Oncodocera*); *latisoma*, new species (subg. *Brachydemina*), figured in Williston (1908); *valida* (Wiedemann), 1830 (as *Anthrax*) [= *eximia* (Macquart), 1850 (as *Anisotamia*)].

Genus *Edmundiella* Becker

Edmundiella Becker, Wiener Ent. Zeitung, vol. 34, p. 347, 1915.
Type of genus: *Edmundiella niveifrons* Becker, 1915, by monotypy.

I have not seen *Edmundiella* Becker. I give a translation of Becker, who describes this genus in these terms:

This diptera species has the characteristics of the group: the antennae which are close together, the non-protruding face, the small, round head with the indentation on the posterior margin of the eyes, and the bisection of eyes as well as the wing venation. It differs in the posterior body, which is strongly and heavily covered with tufts of hair on the sides, whereby it looks much broader than it really is.

This is strongly suggestive of *Ogcodocera* Macquart, it is not impossible that it is the same.

A medium sized, entirely dull black species. Thorax short and distinctly pilose. Head, viewed from the front, circular, viewed from above somewhat broader than long, but not wider than the thorax. Eyes in the male touching or holoptic for a short distance, situated high, bare, indented or excavated on the posterior margin; of the head; the head (occiput) protruding conspicuously (wulstartig). The upper border of the mouth extends to the antenna, so that a facial surface is not present; the distance of the edges of the eyes from each other is scarcely more than one eye width, narrowing toward the bottom. Antennae approaching each other at the base, but otherwise diverging, almost at a right angle; the second segment thickly and heavily pilose, the third lengthened or elongate in the form of a cone, with a small, fine, blunt apex and a delicate short terminal bristle, which is located not quite in the center. Front (frons) densely pilose to below the antennae. Proboscis short, in the example at hand stretched perpendicularly downward, with narrow, insignificant palpi; the base of the proboscis extends to the antenna. Abdomen no wider than the thorax; about twice as long as it is wide, the lateral margins are distinguished by bristle-like tufts of hair, standing far out, so that the abdomen with its fairly dense pile takes up a great width and thus approaches a circular shape. Legs simple, the under side of the femora without bristles. Pulvilli are present; wings long, narrow; the second and third branch of radius forms a slender arch as it opens into the anterior border; it is arched and right angled. The forked vein of the radius takes a course completely parallel to the other. The first posterior cell is opened widely, with parallel longitudinal veins, the small crossvein lies somewhat diagonally and distinctly beyond the middle of the discal cell.

Male. Thorax completely black, the pile somewhat long, gray brownish to black, sides of the pleuron black haired. Haltere brown with a bright stem. Head: back of the head dull black, bare; the whole forehead is covered densely with silver white to gray glittering hairs which are directed downward. At the edges of the eyes there are small black hairs. The upper mouth opening and the second antennal segment are also covered with dense white hairs. Antennae black, in the form as stated above; proboscis and palpus also black. Abdomen completely black, dull, every segment with thick side strands, which consist of black brown hairs accompanied by a few whitish ones, particularly on the anterior segments; on the upper side there are only few hairs, the last segment is black pilose. Sternites bare. Legs completely black. Pile and bristles only delicate. Wings with the aforementioned venation; the basal half is brown, the limitation of the color runs from the end of the first longitudinal vein diagonally over the base of the discal cell and still borders the fifth longitudinal vein.

Length of the body and the wings 6 mm.

A specimen from Greece.

Material available for study: None.

Immature stages: Not on record.

Ecology and behavior of adults: None recorded.

Distribution: Palaearctic: *Edmundiella niveifrons* Becker, 1915.

Genus *Myonema* Roberts

FIGURES 135, 140, 219, 388, 626, 629, 757

Myonema Roberts, Proc. Linn. Soc. New South Wales, vol. 54, p. 563, 1929. Type of genus: *Myonema humile*, 1929, by original designation.

Flies of medium size, characterized by a wing in which there are several features worthy of note. The second vein is almost plane throughout, showing a mere trace of curve; the anterior branch of the third vein shows very little curve at base or apex but does turn up slightly on the outer half; the posterior branch of the third vein is slightly curved backward, the first branch of the medius slightly curved forward so while the first posterior cell is narrowed it is still rather widely open. The hyaline, generalized wing has an anterior border of dark brown extending downward irregularly, in what Roberts (1929) called three "waves." The anterior cross-vein lies before the middle of the broad discal cell; the second vein arises acutely at opposite the base of the discal cell, and the anal cell is widely open. The head in profile is subtriangular, with the eye reniform and extending to the full height of the head, but it does so behind the ocelli and opposite the bilobate occiput. The ocelli are set very far forward, leaving a deep fossa extending for a considerable distance backward to the posterior eye corner. The slightly concave occiput has a deep, central, cuplike recess, but there is no anterodorsal recession of the eye exposing the upper occiput, and there is no indentation and bisecting line at the middle posteriorly.

Finally, it should be noted that the entire head and antennae are much more like that of the Lomatiinae, a fact which Roberts (1929) astutely observed; the short first antennal segment is swollen and has long bristly pile below; the second is of about the same length, a little convex above and below and much less wide; the third segment is conical, a little constricted before the narrow apex, which bears a minute spine. The oragenal cup is moderately prominent and produced above a little beyond the second antennal segment.

This fly is known only from the type-species from Brisbane, Australia.

Length: 10 mm.; wing 9 mm.

Head, lateral aspect: The head is approximately subtriangular in profile because of the oblique anterior extension of the face and oragenal cavity jutting forth beneath the antenna. From its farthest forward point the face rather strongly recedes backward and downward. The eyes reach the full height of the head but only behind the ocelli which are placed anteriorly and upon a raised flattened tubercle; therefore, the eyes extend to a point opposite the bilobate occiput. The face is comparatively small from upper border of oragenal recess to the antennae, but its extent is best gauged from the accompanying figure; it narrows a little below, with the narrowing of the recess.

The antennae are relatively small. The first segment is obtuse and swollen, strongly convex above on which side it bears a few setae and the upper margin is a little longer than the lower, nearly plane margin; below, it bears numerous, dense, slender bristles that are almost as long as the first two segments combined. The second segment is not quite as long as wide, but much less wide than the first segment into which it is rather snugly fitted; it is also tightly attached to the third segment, and it bears a few short setae dorsally. The third segment is as long as the first two segments combined and shaped more or less like a slightly convex cone which strongly narrows beginning at the middle and ends in narrow, slender apex slightly constricted subapically; at the apex is a trace of a very minute stublike micro-segment, which bears a small slender, apical spine. Roberts called it spindle-shaped when viewed laterally, but with its inner surface concave when viewed from above. The palpus is slender and curled and about half as long as the proboscis; it has a short apical segment, the both bear short, fine, erect hairs.

The proboscis is stout and rather short, barely longer, if as long, as the oral recess; the labellum is large; the whole structure may be invisible laterally if tucked into the recess. Its length not longer than the head length. The front and vertex bears a considerable amount of scattered, stiff, erect, fine, bristly hairs perhaps as long as the first two antennal segments; this pile continues opposite the antenna as a downturned fringe of similar hair and continues down along the sides of the upper face and the genal area below to the bottom of the eye.

The occiput is slightly concave but the concavity extends from near the vertex to near the lower point of the eye and is therefore spread out over most of the vertical height of the head; there is no dorsal recession of the eye exposing the occiput as in many other genera of this group. There is no sharp middle posterior indentation or bisecting line on the eye. The occiput bears only a few fine, scattered hairs, the central fringe short.

Head, anterior aspect: The head is nearly as broad as the thorax. Viewed from above, the occiput is raised and bilobate; it has a large, central cavity. In males the eyes are dichoptic, separated by about half the width of the large, rounded, ocellar tubercle, which is situated forward and well below the vertex of the head; ocelli large. Antennae rather close together; first segment distinctly cupuliform.

Thorax: The thorax is longer than broad, almost flat, and clothed with erect and also appressed pile; notopleural bristles are present but weak. The scutellum is wide and semicircular. The mesopleuron has dense, fine, long, bushy pile. The halteres is small and slender and the squama short with a long fringe.

Legs: The legs are slender; the anterior femur has a long, fine fringe of pile; the anterior tibia has 12 fine, black bristles and there are 10 to 12 similar, more distinct bristles on the midtibia; Roberts (1929) calls them spicules. The hind femur is moderately elongate, distinctly dilated distally and bears scattered, long, fine

hairs below. On the distal two fifths, there is a dense brush all around for long, black, subappressed pile, which is longer dorsally and laterally. Pulvilli are present.

Wings: Comparatively narrow and distinctly narrowed basally with both axillary lobe and alula narrow; Roberts (1929) calls the alula absent. There are 2 submarginal cells, but a feature of the wing is the almost plane second vein, and the anterior branch of the third vein is scarcely curved, barely turned up at apex; its posterior branch turns down strongly so that the second submarginal cell is short and rather triangular. The distal cell is broad, the anterior crossvein entering before the middle, the first posterior cell narrows apically from both sides yet is still widely open. The anal cell is widely open. The second vein arises acutely opposite the base of the discal cell. The hyaline wing has a conspicuous anterior border of dark brown extending irregularly downward at three places: basally to fill the whole of first and second basal cells and base of the third basal cell; narrowly over base of discal and fourth posterior cell and whole basal half of first posterior cell, except for a small posterior subbasal clear spot; over all of marginal cell, except apex, and all of first submarginal cell, except apex and a posterior middle clear spot.

Abdomen: The abdomen is obtusely conical; it bears long pile on the sides on the basal half, and with longer, finer, sparser pile posterolaterally and with appressed pale tomentum dorsally. The extreme lateral margins of segments 4 to 7 have thick, long, downturned tufts of short, black, brushlike pile. The eighth segment bears the genitalia; the abdomen broadens to the fifth segment, the remaining ones are decumbent.

Material studied: The series of male types in the Queensland Museum through the courtesy of the Director, Mr. Mack. My illustrations were taken from this series. I also have two females given me by Prof. F. A. Perkins of the University of Queensland.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record. This fly obviously appears early in the spring months, in August and September, mostly August.

Distribution: Australian: *Myonema humile* Roberts, (1929).

Genus *Docidomyia* White

FIGURES 142, 372, 623, 633

Docidomyia White, Papers Proc. Roy. Soc. Tasmania, p. 204, 1917 (1916). Type of genus: *Docidomyia puellaris* White, 1917, by original designation.

Paramonov (1951), pp. 745-746, key to 5 species from Australia.

Small or medium size flies, black and shining in general color. The head is large and more or less globular and very largely given over to the development of the eye. Posterior eye margin quite plane, the occiput not

long, but the occipital lobes contiguous, and the occipital recess deep but small. In the males the eyes are narrowly separated, the vertex quite long, as long as the front, and the small ocellar tubercle situated far forward. The first two segments of the antennae are large, rather bulbous and short, each with tufts of bushy pile. The third segment with small, conical bulb at the base and a slender styloform process a little longer than the base. Below the antennae the face is moderately wide but not protrusive. The oragonal recess is very shallow and triangular above and narrow and extending nearly to the antennae, but both the sides of the face and the oragonal recess slope backward into a deep, steep-walled recess behind. Proboscis stout with short, fleshy labellum. This genus will be rather readily recognized by the slender, attenuate abdomen of reduced size, the hyaline wings narrowed at the base, with the strong apical bend and loop in the second vein.

These flies are restricted to Tasmania and Western Australia.

Length: 6 mm. to 9 mm.

Head, lateral aspect: The head is subglobular, the occiput moderately developed above and below and bears fine, minute micropubescence on both the upper and lower half, and a very scanty fringe of hairs along the circular inner margin of the occipital recess. The eye is very large, occupying most of the head, the posterior margin is entire and plane, the upper facets a little enlarged. The front is convex, distinctly swollen, rather smooth, slightly flattened above the antennae; it has a large, circular, pale colored, hemicircular arch above each antennae. Pile of the front fine and erect and only moderately abundant. The face is very short, from the lateral aspect, no longer anywhere than is the lower front, immediately in front of the antennae, and it slopes rapidly and backward.

The proboscis is extremely short, stumplike with large, fleshy, spinulose, muscoidlike lobes. The palpus is small, elongate, somewhat clavate on the second segment which is about as long as the first segment. The antennae are attached a little below the middle of the head, they are relatively small and short, with the first segment large, obtuse, about as long as wide with dense, short, bushy pile dorsally and medially and with a tuft of longer, dense, bristly pile dorsolaterally and below. The second segment is short and beadlike, or barrel-shaped, almost as wide as the first segment and with a very dense tuft of long bristles dorsolaterally and an equally conspicuous tuft below. Both tufts are directed obliquely outward and downward. Mediolateral surface of this segment only with short setae. Third segment at the base as wide as the second segment, the basal portion somewhat flattened, held obliquely, strongly divergent outwardly and the swollen, basal part about as long as wide. It is abruptly narrowed into a long, stylelike process with a minute, apical spine. This process of the third segment arises dorsally and asymmetrically and is about $1\frac{1}{2}$ times as long as the

bulbar basal portion. Whole third segment densely microscutate.

Head, anterior aspect: The head is more narrow than the thorax and is circular. The eyes are separated in the male and the vertex is extraordinarily long with narrow parallel sides. The width between the eyes is no greater than the width of the third antennal segment. This narrow vertex occupies fully half the distance from the antennae to the posterior eye corners and the short isosceles ocellar tubercle is set very far forward. Front in the female wider than in the male. The face is strongly convergent below, the distance between the eye margins at the bottom of the head a little more than 3 times the width of the very narrow male vertex. The sides of the face, which are lateral to the narrow V-shaped or triangular, upward, wedgelike extension of the oragenal recess, slants sharply beneath the eye margin at the middle of the lower head, so that the eye margins on either side of the short proboscis are deep and quite vertical. The gena appears to be absent, for the sides on the lower part of the oragenal cavity press directly against the eye margin. The slanting part of the face bears considerable long, dense, pale pile up to the point where it drops down below the eye margin. From the posterior view the occiput is strongly bilobed, the dorsal fissure deep, the two lobes touching.

Thorax: The thorax is polished and shining black with rather dense, quite fine, comparatively long, erect pile over the whole of the mesonotum, the notopleuron, the humerus and the disc and margin of the scutellum. There is similar pile on the upper half of the mesopleuron, and such pile is extensive, long, and erect over the whole of the metapleuron leaving the hypopleuron, the pteropleuron, and the sternopleuron bare, except for appressed pollenlike micropubescence. The squama is quite short with a short fringe.

Legs: The legs are comparatively slender, the anterior four femora are a little thicker than the hind pair and all 3 pairs of femora have a ventral fringe of long, erect, fine, stiff hairs. The middle femora also have very abundant similar pile all over the posterior surface. Anterior tibia with numerous, appressed, setate hairs and posteriorly with a row of more or less erect, longer, slender, bristly hairs and a few dorsally. Middle tibia similar. Hind tibia with similar appressed setae and with only a few, short, fine, erect, additional, bristly hairs located principally anteriorly. Pulvilli large, and widely spatulate distally and somewhat notched or bilobed apically. Claws long, sharp, curved at the apex, swollen basally.

Wings: The wings are hyaline, vitreous, narrow at the base with alula absent and axillary lobe narrowed. The first vein ends close to the end of the auxiliary vein. This vein and the costa beyond the costal cell are somewhat thickened and stout. The second vein arises obliquely before the end of the second basal cell and near the apex makes a sharp, downward, or backward fingerlike loop. The anterior branch of the third vein arises rectangularly as a simulated crossvein with a

long backward spur, and the remainder of this vein makes a strong, rounded bend, backward and then forward ending before the apex of the wing. Anterior crossvein enters the discal cell at the outer third. The first posterior cell is open but slightly narrowed, the anal cell is widely open and the ambient vein is complete.

Abdomen: The abdomen is rather small and reduced in size, the first segment is not quite as wide as the thorax, the second much more narrowed, the remaining segments tend to be a little more narrowed with the sides of the abdomen laterally compressed. The pile of the abdomen is scanty, rather fine, and erect with some additional, rather minute, appressed setae over the middle and dorsal portion of the tergites. Male terminalia conspicuous, comparatively elongate, bulbous, and directed obliquely upward.

Material available for study: I have a male of the type-species from Tasmania presented to me by the Commonwealth Scientific and Industrial Research Organization at Canberra, and also other species from Western Australia.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no record of the behavior of adults or of the flowers visited.

Distribution: Australian: *Docidomyia froggatti* Paramonov, 1951; *norrisi* Paramonov, 1951; *puellaris* White, 1917; *swani* Paramonov, 1951; *victoriana* Paramonov, 1951.

Genus *Antonia* Loew

FIGURES 136, 137, 138, 384, 624, 637, 977, 979, 981

Antonia Loew, Neue Beiträge IV, p. 30, 1856. Type of genus:

Antonia suavissima Loew, 1856, by monotypy.

Dimorphophora Walker, Entomologist, vol. 5, p. 272, 1871. Type of genus: *Dimorphophora syrphoides* Walker, 1871, by monotypy.

Dimorphaphus Walker, Entomologist, vol. 5, p. 225, 1871; lapsus. *Dimorphaphus* (Walker).—Loew in Scudder, U.S. Nat. Mus. Bull. 19, part 1, p. 108, and part 2, p. 99, 1882.

Antoniaustralia Becker, Ann. Mus. Zool. St. Pétersburg, vol. 17, p. 458, 1913a. Type of genus: *Antoniaustralia hermanni* Becker, 1913, by monotypy.

Bezzi (1924), p. 137, key to 4 species from Ethiopia.

Paramonov (1929), p. 67, treatment of Palaearctic species.

Engel (1934), p. 358, key to 5 Palaearctic species.

Hesse (1956), pp. 134-143, descriptions, discussion, key to 2 species.

Small to medium-sized flies of rather slender, elongate abdomen, which is more or less tapered and subcylindrical. They are comparatively bare and sparsely pilose and most if not all species show bright reddish and sulphur-yellow markings.

The head is subglobular with deep indentation on the middle of posterior eye margin together with bisecting line among eye facets; reflection of eyes green and red; occiput bilobate above. Antenna short, third segment long and conical with minute spical spine. One of the

most remarkable features in this genus is the sharply conical, anterodorsal extension of the oragenal cup leaving the upper surface beneath the antenna horizontal and the oragenal cup strongly oblique. Equally interesting is the long, slender hyaline wing with the very long, first basal cell, the anterior crossvein located almost at the end of the discal cell; also the second vein and the third vein arise before the end of the second basal cell, with almost no prefurca or radial sector present. There are 3 submarginal cells. The last 3 or 4 tergites are laterally extended and flaplike, the preceding ones rolled tightly around the sternites.

Antonia Loew is a widely distributed genus of the Old World, with 4 or 5 species known from Ethiopia, the same number from the Palearctic, and 2 species from Australia.

Length: 8 to 16 mm.; of wing 8 to 11.5; maximum wing span about 26 mm.

Head, lateral aspect: The head is hemiglobular, the occiput is dense and comparatively long, shorter, flat-appressed adjacent to the eye margin, but becoming more and more erect down to the central fringe around the very large, central cavity. The eye is slightly reniform, although the indentation on the middle of the posterior border, while conspicuous, is not deep. The upper and lower angles of this indentation are equal and there is an unusually long, linear incision horizontally among the eye facets at the bottom of the indentation. Upper eye facets are only slightly enlarged and the whole eye has a brilliant green and red reflection, even in dried material. Front strongly swollen on the lower part to produce a prominent, rounded, villous tubercle bearing posteriorly a shallow, medial fovea or furrow. Pile on the upper part of the front and at the vertex scanty, fine, and erect and not longer than the first antennal segment. Middle of the tubercular swelling with shorter, appressed pile, and lateral flanks of the tubercle with longer pile directed downward. Tubercle quite bare above the antenna. From the lateral aspect the face is short but produced at least as much as the upper part of the frontal tubercle. The oragenal cup, however, is extraordinarily produced, much more than in *Plesiocera* Macquart, and is sharper, conical, and extends nearly as far as the antennal style. Its sides are bare, except for a narrow, oblique band of pile; it is micropollinose below. Orogenal cup sharply separated by a crease from the limited, lateral triangle of the face. The oragenal cup has an indentation laterally at the middle opposite the beginning of the deep, knife-thin, tentorial fissure.

The proboscis is slender, barely extending beyond the epistoma or more usually confined within it; the labellum is long, slender, and pointed. Palpus rather short, slender, composed of 2 segments. It seems to bear only micropubesence. The antennae are attached a little above the middle of the head and occupy a deep cavity between the prominent frontal tubercle and the projecting face. The first segment is large, strongly widened apically, to the greatest extent medially. It is about $1\frac{1}{2}$

times as long as the beadlike second segment, which is distinctly recessed into the cuplike apex of the first segment. Third segment as long or slightly longer than the first two together, not so wide as the second segment, the base distinctly bulblike, abruptly narrowed into a long, thin style. In the material I have seen, the style ends in a comparatively short, slender, spine-tipped microsegment. The first segment bears pile only ventrally and along the sides. The second segment has a tuft of short pile laterally.

Head, anterior aspect: The head is circular though the eyes are a little flattened laterally, and about as wide as the thorax. The eyes are separated in the male by barely more than the width of the strongly swollen, elongate, ocellar tubercle, and anterior to the tubercle the eyes are still more narrowed. Sides of ocellar tubercle vertical. Ocelli are placed in an isosceles triangle distinctly anterior to the posterior eye margin. Posterior eye corners a little rounded backward from the ocellar tubercle. The antennae are widely separated by at least the width of the basal segment. The oragenal cup is quite long, narrow, and very deep anteriorly, scarcely deeper, although strongly widened on a little more than the posterior third. At the point where the oragenal cup is widened the walls are thin and vertical, but in front of this they are strongly inflated inward and flattened and grooved. The walls are also vertical on the anterior part of the oragenal recess. Tentorial fissure long, deep, and very thin. Subocular part of the gena small and triangular. From above, the occipital lobes are distinctly but narrowly separated.

Thorax: The thorax is short, scarcely wider posteriorly, dull black, with, in some species, light gray pollinose vittae, and a grayish triangle of pollen in front of the scutellum. Characteristically the swollen humerus, the somewhat swollen notopleuron and postalar callosity are bright, lemon yellow; mesonotum in some species, including the type-species, with continuous, yellow, lateral margins. The scutellum is wholly yellow or has a quite black basal band, sometimes the corners black. Pile of the mesonotum dense, quite long, brassy yellow, as long as the anterior collar but becoming more sparse posteriorly; also, there is some short, scattered brassy yellow, curled, appressed pile on the disc. Postalar callosity with long, slender, stiff, or slightly bristly golden hairs. Scutellum with similar hairs, which are quite long; no macrochaetae present. Squama short with a fine, short, somewhat banked fringe. Pleuron of no great height, pollinose, lemon yellow with black spots. Mesopleuron chiefly black with dense, small, bristly pile on most of its surface, thinning out anteroventrally. The posterior border of the sternopleuron has long pile. Pteropleuron and hypopleuron without pile but metanotum and the metapleuron in front of the haltere with a large clump of long, erect pile. Curiously there is no pile behind the spiracle. While the propleuron anteriorly has a large, conspicuous clump of long, yellow pile, the prosternum is without pile.

Legs: The legs are slender, only the middle femur and hind femur comparatively stout. Anterior femur, however, slightly widened basally. The first four femora bear a fringe of dense pile posteriorly of no great length and no bristles. Hind femur ventrolaterally with a fine fringe of not very long, stiff hairs but over on its ventromedial surface the hairs are more numerous, oblique, and while slender are almost bristlelike. There are no true bristles present, except 1 or 2 dorsal bristles near the apex on each side, these are yellow in some species. Almost the whole of the lateral surface of the hind femur is covered with flat-appressed, coarse pile. Tibiae long and slender, the anterior tibia with flat-appressed setae; there are 5 of these very small setae postero-dorsally that stand out obliquely, and 6 situated antero-dorsally. Middle tibia similar, the spiculate setae scarcely longer. Hind tibia with flat-appressed, black pile, and with quite small, oblique, yellow bristles of which there are 4 anteroventrally, 5 anterodorsally, and no other rows. However, ventromedially there is a continuation of the curious, black, bristlelike pile found on the inner surface of the hind femur. Anterior tarsi extraordinarily slender, without spicules below. Middle tarsi not quite so slender with 2 or 3 weak spicules on the basitarsi. Hind basitarsi rather strongly spiculate. Claws long and slender, the pulvilli long and spatulate, the arolium minute.

Wings: The wings are hyaline, exceptionally long and slender, narrowed toward the base, the humeral crossvein beyond the midpoint between the base of the wing and radial sector. Radial sector extremely short, almost nonexistent. The second vein arises from a knotlike swelling at the base of the third vein. Auxiliary and first vein very long, the auxiliary vein extending nearly to the outer fifth of the wing. There are 3 submarginal cells, the first posterior cell is rather strongly narrowed apically, the anterior crossvein enters the discal cell at the outer tenth of that cell. Anal cell very widely open. Axillary lobe long and slender but equally wide basally and apically. Alula absent, the ambient vein complete.

Abdomen: The abdomen is about $1\frac{1}{2}$ times as long as the thorax, rather strongly flattened, the sides either nearly parallel and the apex of the male blunt, or somewhat tapered, and ending quite narrowly as shown by Bezzi (1924) in the figure of *Antonia suavisissima* Loew. This appears to be the abdomen of a female, although the head is that of a male and it is labeled a male. The abdomen is rather largely light yellow or red and nearly opaque but in all species with a certain amount of black in the way of opaque black spots, which are either small and triangular and confined to the medial, basal part of the segment, or larger, quadrate, rectangular, extended laterally as a fascia or connecting with lateral black spots, but always with the posterior margins of the tergites linearly yellowish. There are 7 prominent tergites observed from above with an eighth tergite recessed beneath the seventh and the ninth forming a notched, flaplike lid over the genitalia. Last tergite sometimes with a posterior prong or lobe partly encir-

cling the genitalia. Side margins of the tergites extended downward laterally as rounded, thin, overlapping plates. Pile of the abdomen consists of rather abundant, minute, flat-appressed, golden pile with, especially along the posterior half, scanty yet conspicuous, long, erect, partly black, partly golden, bristly hairs, which become even longer but no more abundant laterally. Lateral corners of the first tergite with an unusually loose clump of quite long, erect, stiff, yellow pile. Male terminalia small, the two basimeres lying side by side and exposed apically and ventrally.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of males (as based upon the known males of the two South African species *xanthogramma* and *cercoplecta*) with the basal part more or less divided into two distinct parts, each somewhat shell-like in appearance, ending apically in an outer apical process, the apex of which is bent slightly inwards, each basal part also provided with longish and fairly dense bristly hairs in apical half and on the process; beaked apical joints subtriangular in outline, very much flattened or laterally compressed, the outer face being somewhat concave, ending apically in a fairly sharp point, the lower edge of which is recurved and spine-like, with about 3-4 (or more) longish and stoutish bristles along the upper margin of each, and sometimes also with a few shorter hairs; aedeagal complex with the aedeagus itself short, sometimes provided below with a parrot-beak-like process; lateral ramus, from each basal part on each side, produced together ventrally into a V-shaped ventral process; dorsal part of aedeagal complex produced on each side into a basally directed process; lateral struts shoe-horn-shaped; basal strut remarkable in being four-angled, being produced on each side into a shelf-like or flange-like plate.

Material studied: The type-species in the British Museum (Natural History) and an Australian species, *Antonia rieki* Paramonov. Also a third species presented to me by John Bowden.

Immature stages: Unknown. But Hesse (1956) gives strong evidence that they concern *Bembea* species or masarids, as adults were captured in close association with these wasps.

Ecology of adults: Bezzi (1924) notes the fact that Kneucker captured the type-species in the Sinai Desert on flowers of *Zygophyllum coccineum* Linné. Hesse captured 2 species settling on the damp sand of river beds. There is a harmonizing of color as they rest on some flowers.

Distribution: Palaearctic: *Antonia arenacea* Paramonov, 1934; *armeniaca* Paramonov, 1929; *bouillonae* Séguy, 1932; *fedtschenkoii* Loew, 1873; *persicana* Paramonov, 1936; *suavisissima* Loew, 1856 [= *syrphoides* (Walker), 1871 (as *Dimorphophora*)].

Ethiopian: *Antonia aurata* Bowden, 1959; *bella* Curran, 1927 *cercoplecta* Hesse, 1956; *cirrhatta* Bezzi, 1924; *nigrifrons* Bezzi, 1924; *occidentalis* Bowden, 1959; *xanthogramma* Bezzi, 1924.

Australian: *Antonia decorata* Paramonov, 1950; *hermanni* (Becker), 1913 (as *Antoniaustralia*); *riecki* Paramonov, 1953; *roddi* Paramonov, 1950.

Genus *Aphoebantus* Loew

FIGURES 126, 205, 213, 227, 369, 405, 706, 719, 906, 907

Aphoebantus Loew, Berliner Ent. Zeitscher., vol. 16, p. 77, note, 1872. Type of genus: *Aphoebantus cervinus* Loew, 1872, by monotypy.

Triodites Osten Sacken, Bull. U.S. Geol. Surv., vol. 3, p. 245, 1877. Type of subgenus: *Triodites mus* Osten Sacken, 1877, by monotypy; preoc. Gistel, 1848.

Triodytus Riley, American Ent., vol. 3, p. 279, 1880b; lapsus.

Aphoebantus Loew, in Scudder, U.S. Nat. Mus. Bull., part 1, p. 27, 1882; lapsus.

Aphoebantus Hyslop, Proc. Ent. Soc. Washington, vol. 14, p. 103, 1912; lapsus.

Cononedys Hermann, Zeitschr. für system. Hymenop. und Dipt., vol. 7, p. 197, 1907. Type of subgenus: *Anthrax stenura* Loew, by original designation. *Conogaster* Hermann = *Cononedys* Hermann, see Bezzi 1924.

Triodina, new subgenus. Type of subgenus: *Triodites mus* Osten Sacken, by present designation.

Meganedys, new subgenus, type of subgenus, *petiolata*, new species.

Coquillett (1891c), pp. 254-256, key to 24 species from southwestern U.S.

Coquillett (1894a), pp. 105-107, key to 28 species of southwestern U.S.

Bezzi (1925), pp. 203-205, key to 9 Palaearctic species.

Engel (1934), pp. 397-398, key to 10 Palaearctic species.

Maughan (1935), p. 69, key to 4 species from western U.S.

Melander (1950a), pp. 15-21, key to 64 species and subspecies from U.S.

The genus *Aphoebantus* Loew was based upon an American species, *cervinus* Loew, which is before me, together with many other Nearctic species. These flies are relatively small and characterized by the rather slender, somewhat elongate, and always tapered abdomen. The general coloration is almost always black with thin grayish white pollen although legs may be in part yellowish and the appressed pile of slenderly flattened scalelike hairs or tomentum and other more erect hairs is usually white or yellowish brown. The antennae are short, the third segment with bulbous or sometimes subtriangular base that is produced into a slender bristle-tipped style. Generally the males have a more silvery head. The head is large, subglobular, easily detached, and males are holoptic; the occiput is only moderately developed. Scutellum sometimes bilobed. They are distinguished from the related *Epacmus* Osten Sacken by the quite short mouthparts and the less slender antennal style; in *Epacmus* Osten Sacken the stylar part of the third segment is abruptly formed and very slender, often with a twisted or semihooklike apex, and pulvilli are absent. In *Aphoebantus* Loew pulvilli are generally well developed. Characteristically the male hypopygium is large and prominent, protrusive posteriorly; they furnish excellent specific characters. Wing hyaline, or rarely smoky toward base, with only 2 submarginal cells; apex of marginal cell slightly and characteristically dilated ventrally; base of second submarginal cell sometimes rectangular, with basal spurvein. This genus appears to have its greatest development in the southwestern part of the United States. It is also known from the Mediterranean and Ceylon.

Length: 3 to 10 mm., most species in between. Wing 4 to 10 mm.

Included in *Aphoebantus* Loew is the distinct new subgenus *Triodina*, in which the males and often the females have rather dense, erect, very fine, long, upstanding pile upon the abdomen and no flattened hairs or tomentum. Pulvilli present or absent.

Included also is the new subgenus *Meganedys*, with first posterior cell closed and with a long stalk; proboscis slender and elongate; pulvilli short but present, rounded, abdomen rather wide; antenna as in *Aphoebantus* Loew. The type will be *petiolata*, new species, southwestern United States, the name derived from the stalk of the first posterior cell.

Melander (1950) has ably discussed the phylogeny of the genus with its related forms including *Eucessia* Coquillett. Even though in many respects there is an overlapping of characters, these genera, or subgenera, are very useful. Possibly a more extended study, with dissected genitalia may show the need for further subdivision. Also the presence of so many species in the California and Arizona area suggests that here we have a generic complex of recent origin undergoing perhaps considerable phylogenetic differentiation at this time.

Also I place *Cononedys* Hermann (1907) as a subgenus of *Aphoebantus*. It is distinguished by the presence of 2 distinct apical microsegments at the end of the third antennal segment.

American species of *Aphoebantus* Loew may be described in the following way.

Head, lateral aspect: The head is subglobular with very prominent occiput in both sexes, but especially in the female, the occiput is bilobate above with narrow, paper-thin fissure. Posterior eye margin distinctly indented with minute anterior notch, with the extent of the indentation variable. Occiput either thinly or densely pollinose, the pile largely consists of numerous, flattened scales scattered over the lateral border and a scanty fringe of short, erect hairs along the inner rim. The front is convex, nearly plane, with the eye near the vertex, very slightly swollen in some species. In other species the front is more strongly swollen on the lower half in front of the antennae. The front is generally pollinose and the pile erect and abundant or sparse and bristly with sometimes patches of flattened, scalelike hairs laterally. In other species the whole front is covered with comparatively numerous bristles, at least as long as the first segment of the antennae and all of them curved forward. In *Aphoebantus vittatus* Coquillett the scales on the sides of the front are rather thick, broad, matted, and silvery white. The face in profile beneath the antennae is long vertically and extends a considerable distance beneath the antennae.

The proboscis is extremely short and stout with robust, stout, swollen, fleshy labellum. In no species before me is it longer than the oragenal recess. Palpus slender, long and cylindrical, with comparatively long bristly hairs laterally and at the tip. The antennae are small, attached to the middle of the head. The first seg-

ment is very short, at least twice as wide as long, it bears a few long setae ventrally, shorter setae dorsally and on the sides. The second segment is even shorter, only about half as long as the first. The third segment is bulblike at the base, swollen until it is distinctly wider than the second segment, then suddenly and abruptly narrowed medially so that on the outer edge there is a long, conical process, rather slender and about twice as long as the basal part and bears a spine at the apex. If the fly is rotated the asymmetry of this antennal process is not apparent, and it appears to be abruptly narrowed from both sides of the segment. The third segment bears a small spine apically.

Head, anterior aspect: The head is circular, the head is wide or slightly wider than the thorax. The eyes in the male are holoptic for a distance which may be as much as half the length of the front or as little as one-fourth the length of the front. Eyes a little sunken and depressed where they meet. The female front is wide, converging above, and the vertex is not quite 3 times as wide as the width of the ocellar tubercle. The large ocelli rest on the sides of a swollen tubercle with vertical, lateral, and posterior margin placed in a short isosceles triangle and with a tuft of fine, bristly hairs arising on the tubercle. The antennae are quite widely separated by a distance equal to the length of the first two antennal segments and sometimes even more widely separated. The oragonal recess is elongate oval extending back below nearly to the posterior eye margins so that much of the buccal cavity is ventral. In profile the buccal cavity is gently oblique. The cavity is deep with the inner walls vertical, the genae are narrow and linear and with a shallow tentorial fissure near the middle.

Thorax: The thorax is short and compact. The mesonotum is low, very little convex, a little more so in some species. The scutellum is quite large, more or less flattened on the disc, sometimes very thick and convex apically, usually shining, and more shining in the mesonotum and varying from faintly pollinose to polished black. Pile of mesonotum varies from rather dense, flat-appressed, somewhat elongate, scaliform hairs, which are very easily rubbed off leaving a denuded surface. This appressed vestiture may be intermixed with scattered, fine, long, erect, or semierect, bristly pile, and there is generally a collar of erect pile across the anterior margin of the mesonotum. The humerus varies from faintly to densely pollinose and from sparsely to quite densely pilose. Notopleuron with several bristles of varying stoutness but rarely as strong as the macrochaetae sometimes found on the apex of the scutellum. Upper half of mesopleuron with long, coarse, or slightly flattened pile curled upward, the lower half with appressed pile or scales. Sternopleuron with appressed scales or with erect, coarse pile as in the type-species. Pteropleuron, metanotum, anterior metapleuron pollinose only. There is a dense tuft of pile on the posterior metapleuron behind the spiracle. Propleuron laterally with a tuft of long pile and the pro-

sternum with pile and scales. Squama moderately large with a short, fine, sparse fringe.

Legs: The femora are relatively short, the hind femur is stout and sometimes very slightly thickened through the middle. The middle and anterior femur may be slightly thickened but is more slender toward the apex. All the femora often with comparatively dense, broad, distinct, flat-appressed scales. Anterior femur with or without a posteroventral fringe of 3 to 8 slender bristles located principally on the outer half. On the middle femur the bristles are stouter, more distinct, apt to be entirely restricted to the outer half, and in addition to those on the posterior row there are 1 to 3 bristles weak or stout on the anteroventral surface. Hind femur with 3 to 8 stout bristles posteroventrally, sometimes restricted to the outer half, again extending closer to the base. Anterior tibia quite slender, as long as the femur, with smaller, flattened scales or with only appressed setae. In the type-species there are present 3 or 4 stout, anterodorsal bristles and 4 or 5 stout posterior bristles, but in some species there is only a row of 6 to 10 small, suberect setae dorsally but with a few stout bristles posteriorly. Middle tibia with quite stout and long dorsal and posteroventral bristles and with shorter, posterior, and anteroventral bristles in the type-species. In other species the tibial bristles are short and much less conspicuous. Again on the hind tibia in the type-species there are 3 prominent rows of bristles, an anteroventral, an anterodorsal, and a posterodorsal, each containing 5 elements. Similarly the number and strength of these bristles vary in other species. Tarsi comparatively short, the pulvilli nearly as long as the claw and rather slender. Claws slender, sharp, curved from the base. The legs in *Aphoebantus* Loew vary from dark reddish brown to black on the femora with the tibia and tarsi usually very dark brown and sometimes brown or even light yellow.

Wings: The wings are vitreous hyaline. There are 2 posterior cells. Sometimes, as in the type-species, a strong spur extends backward from the end of the plane, crossveinlike basal section of the anterior branch of the third vein. Absent, or only faintly indicated in the type-species, there is usually a weak but distinct bend in the second vein a little beyond the furcation of the third vein so that the apex of the marginal cell is elongate, rounded, and bent downward like the shape of the apical segment of a finger. The anterior crossvein enters the discal cell at or slightly before or slightly after the middle of the discal cell. There are 4 posterior cells. The first posterior cell is distinctly narrowed at the apex and slightly widened in the middle. Anal cell widely open, axillary lobe and alula wide, base of costa distinctly expanded with a costal comb of setae and with a prominent, flattened, apical spur. The second vein arises at a sharp angle near the base of the discal cell or across from it. Ambient vein complete.

Abdomen: The abdomen is usually elongate and distinctly tapered, its length a little greater than that of the thorax including the scutellum, but in some species

actually less in length. Viewed from above the sides of the abdomen tend to be plane, slightly concave, or slightly convex. The color is usually black and shining covered with a variable amount of flat-appressed, scale-form pile of sometimes contrasting colors, often together with a postmarginal fringe of fine, semierect, bristly hairs, which sometimes instead of being erect tend to be curled downward and backward and not readily distinguished from the remaining pile. They may be lacking or restricted to a few hairs near the posterior corners. Characteristically there is a band of dense, coarse, erect, spikelike pile on the outer third of each side of the first segment. Sternal pile rather similar to the tergal pile. Abdomen sometimes more or less flattened, or distinctly cylindrical or compressed laterally. In females there are 7 tergites with the seventh generally compressed laterally, and there is a dense fringe of shining, bristly or slightly flattened pile curled inward around the female terminalia. Male terminalia distinctly large and protrusive.

The male terminalia from dorsal aspect, epandrium removed, show a figure that is broad basally. The basistylus narrows conspicuously on the outer half. The epiphallus is very short. The basal apodeme is extraordinarily large and long, and at least as large as the whole epandrium. The dististyli are small with a curved, apical hook, which viewed from above is curved outward, viewed laterally is curved upward and backward. The epiphallus is strongly separated dorsally from the ejaculatory process. Epandrium is more or less triangular.

Material studied: Besides a female of the type-species given me many years ago by R. H. Painter, I have a large series of many species collected by me and by Marguerite Hull in the southwestern United States.

Immature stages: The larvae of this genus consume the egg pods of locust, and at least one species is known to be a parasite of *Tiphia* wasps in India. See discussion under life histories.

Ecology and behavior of adults: The adults are usually found resting on the ground, on the sand, and sometimes on rocky surfaces, but may be uncommonly found on flowers. Melander (1950) has recorded them on creosote bushes, *Larrea divaricata*, *Wislizenia refracta*, *Heliotropium* species, *Gilia*, *Phycelia*, and *Cryptantha* species, on *Adenostoma*, wild buckwheat or *Eriogonum fasciculatum*, *Lotus* and *Hugelia* species.

Distribution: Nearctic: *Aphobebantus abnormis* Coquillett, 1891; *altercinctus* Melander, 1950; *arenicola* Melander, 1950; *balteatus* Melander, 1950; *bisulcus* Osten Sacken, 1887; *borealis* Cole, 1926; *brevistylus* Coquillett, 1891; *capax* Coquillett, 1891; *carbonarius* Osten Sacken, 1887; *catenarius* Melander, 1950; *catulus* Coquillett, 1894; *cervinus* Loew, 1872; *concinus* (Coquillett), 1892 (as *Epacmus*); *contiguus* Melander, 1905; *contiguus separatus* Melander, 1950; *conurus* Osten Sacken, 1887; *cyclops* Osten Sacken, 1887; *denuatus* Melander, 1950; *desertus* Coquillett, 1891; *eremicola* Melander, 1950; *fucatus* Coquillett, 1894;

fumidus (Coquillett), 1891; *fumosus* Coquillett, 1892 (as *Epacmus*); *gluteatus* Melander, 1950; *halteratus* Melander, 1950; *hians* Melander, 1950; *hirsutus* Coquillett, 1886; *inermis* Coquillett, 1891 (erratum for *abnormis*); *interruptus* Coquillett, 1891; *inversus* Melander, 1950; *leiviculus* Coquillett, 1894; *maculatus* Melander, 1950; *marcidus* Coquillett, 1891 [= *squamosus* Coquillett, 1891, males only]; *marginatus* Cole, 1923; *micropyga* Melander, 1950; *mixtus* Coquillett, 1891; *mormon* Melander, 1950; *mus* (Osten Sacken), 1877 (as *Triodites*; subg. *Triodina*), *mus barbatus* Melander, 1950; *obtectus* Melander, 1950; *parkeri* Melander, 1950; *pavidus* Coquillett, 1886; *pellucidus* (Coquillett), 1892 (as *Epacmus*); *poedus* Osten Sacken, 1887; *rattus* Osten Sacken, 1887; *scalaris* Melander, 1950; *schlingeri* Hall, 1957; *scriptus* Coquillett, 1891; *sperryorum* Melander, 1950; *squamosus* Coquillett, 1891, females only; *tardus* Coquillett, 1891; *timberlakei* Melander, 1950; *transitus* (Coquillett), 1886 (as *Leptochilus*); *ursula* Melander, 1950; *varius* Coquillett, 1891; *vasatus* Melander, 1950; *vittatus* Coquillett, 1886; *vulpecula* Coquillett, 1894.

Neotropical: *Aphobebantus argentifrons* Cole, 1923; *dentei* d'Andretta & Carrera, 1952.

Palaeartic: *Aphobebantus albicinctus* Paramonov, 1925; *armeniacus* (Paramonov), 1925 (as subg. *Cononedys*); *armenicus* (Paramonov), 1929, nomen nudum (as subg. *Cononedys*) [= *armeniacus* Paramonov, 1929]; *bituberculatus* (Becker), 1915 (as subg. *Cononedys*); *claripennis* Becker, 1903; *clauseni* Aldrich, 1928; *costalis* Paramonov, 1929, *costalis subcostalis* Paramonov, 1929; *dichromatopus* Bezzi, 1925; *efflatouni* Bezzi, 1925; *erythrasis* (Hermann), 1907 (as subg. *Cononedys*); *escheri* Bezzi, 1908; *latifrons* Paramonov, 1929; *persicus* Becker, 1912; *pusillus* Paramonov, 1929; *scutellatus* (Meigen), 1838 (as *Anthrax*); *seratus* Aldrich, 1928; *sternurus* (Loew), 1870 (as *Anthrax*) [type of *Cononedys*]; *transcaspicus* Paramonov, 1929; *turkmenicus* Paramonov, 1929; *wadensis* Bezzi, 1925.

Ethiopian: *Aphobebantus bilobatus* Bezzi, 1924.

Oriental: *Aphobebantus ceylonicus* (Brunetti), 1909 (as *Argyromoeba*).

Genus *Epacmus* Osten Sacken

FIGURES 141, 143, 628, 631, 913, 914, 915, 916, 917

Leptochilus Loew, Berliner Ent. Zeitschr., vol. 16, p. 78, nota.

1872. Type of genus: *Leptochilus modestus* Loew, 1872, by monotypy.

Epacmus Osten Sacken, Biologia Centrali-Americana, Dipt., vol. 1, p. 142, 1887. Change of name.

Coquillett (1892a), p. 9, key to 5 species from the western United States.

Melander (1950a), pp. 5-6, key to 12 species from the southwestern United States.

Small or medium-sized flies with tapered, cylindrical, or compressed abdomen, which are very similar in general appearance to *Aphobebantus* Loew and are distinguished by the produced face, the relatively long

proboscis that to a variable extent extends beyond the confines of the oragenal recess and has a longer, slender, nonfleshy-type labellum.

Several South African genera within this tribal complex also have a peaked or produced face, but without exception they are separated by the manner of origin of the second vein, which arises abruptly, far distal to the base of the discal cell.

The antennal style in *Epacmus* is as a rule unusually slender and long, strongly differentiated from the basal bulblike portion, and the thornlike spine or bristle at the apex is frequently curved up after a characteristic fashion. The pulvilli are variable but are very often much reduced, almost vestigial.

Epacmus is a characteristic element of the bombyliid fauna of the western United States; the 12 species range from Washington to California, a few as far east as New Mexico or extreme western Texas.

Length: 9 to 9 mm.; wing 5 to 8 mm.

Head, lateral aspect: The head is subglobular, the occiput only moderately extended above and behind the vertex and equally prominent below. It bears dense, broad, flattened scales that extend to the eye margin over a pollinose surface. The marginal fringe along the inner edge of the occipital recess is not only quite fine but very scanty. The posterior eye margin is distinctly though rather shallowly indented and has a small, triangular notch in the eye facets. The eyes are more prominent on the upper half than below. The front is convex, not at all extensive and bears scattered, scalfiform hairs and is generally densely pollinose, often silvery, or may be golden in color. The face is triangularly produced forward but somewhat obtusely, and is generally covered rather densely with shining, pale pollen or micropubesence, some of it scalelike. Sides of the oragenal cup rather prominent, polished and bare. Proboscis elongate and slender, longer than the head and distinctly much longer than the oragenal cup. The palpus is very slender, threadlike, elongate with 2 or 3 fine hairs on the apical segment, which is only about one-fourth as long as the basal segment. The antennae are small, the first segment is much shorter than wide, considerably wider apically, rather cup-shaped, not greatly produced medially, a little more so laterally and the second segment, which is about the same length, is widely and solidly attached. The second segment is more than twice as wide as long with the sides rounded and convex. The first segment has a tuft of setae dorsolaterally, a few minute setae ventromedially and below, the second segment has similar pile and setae similarly placed. The third segment is formed as a low, compact bulb sharply contracted into an asymmetrical, long, slender, pronglike lobe which arises on the lateral edge of the third segment. It bears apically an oblique, long, conical microsegment.

Head, anterior aspect: The head is not quite circular; it is somewhat subquadrate. The head is about the same width as the thorax. The eyes are holoptic in the male for a short distance, which is usually not much

greater than the length of the ocellar tubercle, hence the front is large as well as convex. The eyes are a little sunken where they meet and the rather small, conspicuous ocellar tubercle is nearly equilateral. The ocelli rest on the eye margin and the eyes viewed from above are curved forward on their upper posterior margins. The female has the eyes more widely separated. The antennae are widely and clearly separated by a distance nearly equal to the width of the first antennal segment. The oragenal cup is comparatively short, slightly widening anteriorly, the upper half of its inner margin slopes strongly and the lower portion has vertical walls. The ventral and dorsal ends of this recess are both distinctly triangular, the one extended forward, the other extended backward. The genae are confined to a narrow, pollinose line along the eye margin. Tentorial fissure absent. The occiput viewed posteriorly is bilobate with the adjacent lobes touching; the fissure between is deep but without any additional pocket anteriorly.

Thorax: The thorax is short and compact; the mesonotum is as wide as long, rather low and flattened, sometimes moderately shining and in some species partly or wholly opaque pollinose. The mesonotum is widely and rather densely covered with loose, comparatively wide, long, lanceolate scales. They are apt to be rubbed off over the middle part of the mesonotum, but they adhere to the whole notopleuron, humerus, and postalar callosity. Scales are generally present also on the scutellum, unless rubbed off. Pollen of mesonotum often vitate. There are sometimes a few, very slender, erect, long hairs on the notopleuron and always 2 or 3 long, slender bristles. Margin of scutellum with several irregularly placed hairs or slender bristles and some other long hairs on the disc. A few species have the postscutellar margin with 4 pairs of comparatively stout, long bristles, and the margin indented in the middle and bearing scales. Postalar callosity sometimes with 3 or 4 long, conspicuous bristles. Pleuron pollinose, the upper half of the mesopleuron with a rather dense band of upwardly turned bristles and scales and in the posterior corner with a conspicuous, backwardly turned tuft containing mostly scales but with some hairs. Lower part of mesopleuron with a few loose scales; upper half of sternopleuron with a large, dense patch of appressed scales. Pteropleuron, metanotum, and hypopleuron pollinose only. However, the metapleuron in front of the halteres, and posteriorly behind the spiracle have either a small patch of scales or a dense, wide patch of long, coarse pile. Squama large with a long, fine fringe on the medial portion and the outer part with a wide, plumelike border of long, extensive hairs which varies greatly in different species.

Legs: All of the femora are rather stout, especially the last four, the anterior pair varying in thickness. All pairs covered rather densely with long, appressed, more or less truncate, shinglelike scales. The anterior femur has a few semierect, bristly hairs of no great length posterodorsally and sometimes with 5 or 6 rather stout

bristles anteroventrally. Middle femur similar with a row of 4 or 5 posteroventral and a like number of somewhat stronger anteroventral bristles. Hind femur with 3 or 4 strong, ventral bristles on the basal half, and on the outer half of the hind femur there are 3 to 5 stout, anteroventral and 1 to 2 posteroventral bristles. Sometimes there are 2 or 3 dorsoapical bristles. All of the tibiae are quite long and slender. They have small, appressed scales, the anterior pair has a few quite appressed, small setae and 3 or 4 posteroventral, short bristles; in some species the bristles are more conspicuous. Middle tibia with 3 or 4 stout bristles anteriorly, 4 or 5 posteriorly. Hind tibia with 4 rows of stout, rather long, oblique bristles. There are 3 or 4 anteroventrally, 5 or 6 anterodorsally, 5 or 6 dorsomedially and a like number ventromedially. Tarsi long and slender with short, ventral bristles and longer ones apically. The claws are only slightly and gently curved from base to apex. They are long, relatively blunt at apex, and the pulvilli are greatly reduced.

Wings: The wings are hyaline, elongate, and rather slender. There are 2 submarginal cells, the anterior branch of the third vein arises usually plane and simulating a crossvein, with or without a backward spur. The marginal cell is slightly but gradually widened apically, has at most a slight preapical bend, but is usually blunt at the apex. The second vein meets the costa at a right angle. First posterior cell open but to a varying extent; in those species where it is more widely open the first bend of the anterior branch of the third vein tends to be rounded. The anterior crossvein enters the discal cell at or slightly beyond the middle. The second and third veins fork acutely opposite or before the base of the discal cell. Anal cell widely open, ambient vein complete, the alula small but rather wide.

Abdomen: The abdomen is longer than the thorax, in males subcylindroid, but rather compressed laterally, especially through the middle so that viewed from above the sides are often concave. In females the abdomen tends to be elongate, conical, and distinctly tapered, the third and fourth tergites only slightly more narrow than the first two, the fifth to seventh more strongly narrowed. I find 7 tergites in the females and 8 in the males with the eighth tergite quite short. The pile consists of rather dense, large, coarse, appressed or partly erect scales which are more prominent on the sides of the tergites and more apt to be rubbed off dorsally and medially. In both males and females there is a conspicuous band of long, dense scales or scaliform hairs; appressed along the posterior margin of the first segment and changing to a wide tuft of dense, long, erect, spikelike pile laterally. Females of some species have dense, black scales on the tergites with a narrow white or yellow fringe of scales along the posterior border overlapping the next tergite. In addition both sexes have a considerable amount of fine, erect, long pile laterally on the tergites. Female terminalia surrounded on all sides by a dense fringe of shining, bristly

pile curled inward. Male terminalia somewhat enlarged and clublike, enclosing the two prongs of the aedeagus.

The male terminalia from dorsal aspect, epandrium removed, show a figure similar to *Aphoebantus* Loew. It is much broader, wider, short and compact. The dististyli are similar and turn outward. The epiphallus is shortened, the epandrium is quadrate. The basal apodeme much smaller and shorter from the lateral aspect, more or less concealed by the epandrium. Just as in *Aphoebantus* Loew, the ejaculatory process is well separated from the overlying epiphallus.

Material studied: A male of *Epacmus litus* Coquillett lent me by Jack Hall and males and females of several species recently collected by the author in the Southwest.

Immature stages: Unknown. Probably similar to *Aphoebantus* Loew.

Ecology of adults: Similar to *Aphoebantus* Loew, generally found resting on sandy or rocky ground.

Distribution: Nearctic: *Epacmus cirratus* Melander, 1950; *chunalis* Melander, 1950; *connectens* Melander, 1950; *labiosus* Melander, 1950; *litus* Coquillett, 1886; *modestus* (Loew), 1872 (as *Leptochilus*); *morsicans* Melander, 1950; *nebritus* Coquillett, 1894; *nitidus* Cole, 1921; *pallidus* Cresson, 1919; *ponderosus* Melander, 1950; *pulvereus* Melander, 1950; *tomentosus* Melander, 1950.

Genus *Pteraulax* Bezzi

FIGURES 123, 382, 625, 630

Pteraulax Bezzi, Ann. South African Mus., vol. 18, p. 117, 1921a.

Type of genus: *Pteraulax flexicornis* Bezzi, 1921, by original designation.

Hesse (1956). pp. 336-338, key to 7 species.

Small flies strongly resembling *Aphoebantus* Loew; however, there are 3 submarginal cells and the first posterior cell is closed; and the hyaline or nearly hyaline wing is strongly wrinkled, the anal cell open, and pulvilli present. The eyes of the male are holoptic. These dark colored flies are characterized further by pale pile, and a narrow, elongate, cylindrical abdomen; however, the abdomen is no longer than the thorax. The abdomen has conspicuous, flat-appressed, broadly scalelike pile; the posterior margins of the tergites bear lateral fringes of long, stout, bristly hairs; legs with conspicuous bristles.

Pteraulax Bezzi is a small genus of at least 7 South African species.

Length: 7 to 11 mm.

Head, lateral aspect: The head is more or less hemispherical, the occiput is only moderately developed posteriorly; as in related genera there is a deep central recess bordered with only extremely short hairs. It is bilobate above the narrow, medial fissure. Laterally the occiput bears flat-appressed, narrowly scaliform hairs. There is a deep, conspicuous indentation on the poste-

rior eye margin accompanied by a bisecting line or shallow crease. The face is rounded and very little produced forward. Its surface, together with the front, is pollinose and broken by tiny, punctate bare spots. The face bears only loose, scattered, erect, moderately long sometimes bristly pile, but among the similar coarse pile of the front there are some 40 to 50 conspicuous, rather wide, pale, brownish yellow scales which are suberect. The ocular margin of both front and face are narrowly bare, except for pollen. The oragenal cup is scarcely in evidence at all in the profile aspect, and it does not extend onto the face proper. The lower face is bluntly and broadly rounded and pollinose, extending over into the oral cavity. However, just above the proboscis there is a narrow, cuplike rim of very limited proportions set almost against the eye margin and separated from it by the usual crease. Palpus exceptionally fine, long and threadlike and composed of 2 segments; the apex is a little swollen and both segments bear a few long, scattered hairs. The stout proboscis is subcylindrical, shining, nearly bare, a little arched upward and slightly longer than the oral cavity. The short, stout labellum is wider, more or less muscoidlike.

The antenna is attached at the middle of the head, or barely above it; the antenna is short and stout, the first segment 2 or 3 times as long as the second and nearly twice as wide at its apex as the second segment. This segment bears the characteristic medial extension or protuberance found in related genera. The third segment is wide, broad basally, pyriform and produced on the outer half into a rather stout styliform piece, which carries a minute, short microsegment, which is truncate apically.

Head, anterior aspect: The head is wider than the thorax with the face and front continuous and relatively narrow, comprising little more than one-fourth the head width. The oral opening is approximately $2\frac{1}{2}$ times as long as wide, a little narrowed in the middle, since the walls of the very low oragenal cup bend inward. The eye margins very slightly converge so that the sides of the face are not quite parallel. There is a small area of conspicuously enlarged facets on the eye where the eyes meet. The antennae are separated by the apical width of the first segment. The ocelli are distinct and set upon a low, anteriorly segregated tubercle.

Thorax: The thorax is slightly longer than wide with a rather short, scanty collar of coarse pile along the anterior margin but including the humerus. The notopleural and nearly all of the mesonotal pile is subappressed, or flat-appressed and more or less coarse and wiry with a few much finer, erect hairs intermixed. The scutellum is covered with similar pile, flat-appressed also, but distinctly more flattened and somewhat scalelike, but not forming the conspicuous scales present on the abdomen; the margin of the scutellum with a few longer, stiff hairs or even bristles. The notopleuron has 1 or 2 unusually stout, long bristles; postalar callosity with 2 more slender bristles; the outer squamae are

extensive, thin and flaplike. The pleuron is bare, except for a tuft of bristly hairs along the dorsal border, a more dense tuft of less bristly hairs in the upper anterior corner which grades into finer hairs below. Oddly, the mesopleuron bears a few scattered scales, the sternopleuron has a conspicuous, dense patch of flat-appressed scales. The pteropleuron, the metapleuron in front of haltere, and metasternum, and all of the hypopleuron above the middle coxae usually bare; there is a dense tuft of scales below the spiracle, another smaller tuft in front of the posterior coxa.

Legs: All of the femora are somewhat stout and slightly swollen and are 3 or more times as thick as their corresponding, uniformly slender tibiae. In addition the hind femur bears a double row of conspicuous bristles, 5 on the ventrolateral margin, 3 on the ventromedial margin confined to the basal half; otherwise the pile of the legs is distinctly composed of rather broad, plastered, flat-appressed, pale scales. The anterior tibia has a posterior row of 6 long spicules and an anterior row of some 10 short spicules; middle tibia has similar spicules; hind tibia has 4 rows of rather longer, bristlelike spicules, each row containing only 3 or 4 elements. The claws are long, quite slender, the pulvilli well developed; arolium minute and stublike; dorsal apex of last tarsal segment with a stout, black, spinal seta; ventral surface of last 4 tarsal segments with dense, erect, short, black, spinous setae.

Wings: The wings are rather small, a little wider apically, the anterior branch of third vein sigmoid; 3 submarginal cells present, the first posterior cell is closed and stalked; anal cell is open, alula well developed, the ambient vein is complete. The wings are hyaline but the surface bears fluted ripples especially anteriorly. The subcostal vein ends close to the end of the second vein and the anterior crossvein enters the discal cell near the middle; costal setae small.

Abdomen: Although the abdomen is elongate, tapered, cylindrical and blunt at the male apex, it is rather small and is shorter than the thorax if the large scutellum is included. The first segment is nearly twice as wide as the apex of the abdomen, and bears a band of rather dense, erect, long, quite coarse pile, which is, however, confined to the outer third and is long laterally as well. The posterior margin of this tergite has an appressed fringe of flattened pile. Remaining tergites rather densely covered, especially laterally, with flat-appressed, narrow scales directed more or less medially. Also laterally the posterior margins bear 4 to 6 conspicuous, long, erect slender bristles or bristly hairs; sternites with a few similar bristles, and the posterior margin of the last tergite and sternite bears a conspicuous fringe of 7 or 8 long, dark, bristly hairs, or even stout, long bristles.

Male terminalia enlarged, directed backward and plane with the axis. I quote Dr. Hesse's description of the terminalia based on males of many species.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium with the sternite opposite it well developed, broad, its apical angles more or less rectangular, sometimes rounded, and its hind margin not incised, sometimes broadly emarginate; basal parts of hypopygium with a small triangular tergite dorsally between their bases, dorsal part in neck region almost without or with only very fine and short hairs, the dorsal apical part sometimes with a lobe-like process, the outer lower edge or margin of each basal part sometimes produced into a lobe-like or even triangular process; beaked apical joints laterally compressed, either elongate, almost blade-like, or bird-head-shaped from side, covered with shortish hairs, the apex usually curved downwards; a distinct, conspicuous, ventral aedeagal process or apparatus present and formed by the lateral ramus on each side from each basal part coalescing apically to form a projecting rod-like or beak-like process on which there is a transverse slit-like groove or incision through which or in which the apex of aedeagus opens; basal part of ramus on each side where it joins each basal part produced into a process or broad leaf-like extension; lateral struts comparatively broad, shoe-horn-shaped or scapula-like.

Material studied: Representatives of *flexicornis* Bezzi in British Museum (Natural History) and a pair of *setaria* Hesse kindly sent by Dr. Hesse for study and dissection.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Pteraulax ausana* Hesse, 1956; *braunsi* Bezzi, 1922; *cinctalis* Hesse, 1956; *eremophilus* Hesse, 1956; *eurymetopa* Hesse, 1956; *flexicornis* Bezzi, 1921; *latifacies* Hesse, 1956; *setaria* Hesse, 1956.

Genus *Pteraulacodes* Hesse

Pteraulacodes Hesse, Ann. South African Mus., p. 348, 1956a.

Type of genus: *Pteraulacodes karoensis* Hesse, 1956, by original designation.

This is a genus of small, *Plesiocera*-like flies that have a relatively elongate, tapered abdomen; consequently they also resemble the Holarctic genus *Aphobantus* Loew. Hesse (1956) notes that it resembles both *Plesiocera* Macquart and *Stomyliomyia* Bigot, especially the latter genus, and may be distinguished from both by the absence of a well-marked facial cone, the bisected hind margins of the eyes, the longest and slender terminal element and style of the third antennal segment, the slender and bristlelike spines on the hind femur, and bristlelike spicules on the outer part of the tibiae, etc. Moreover, it is separated further from *Plesiocera* Macquart by the presence of 3 submarginal cells.

Pteraulacodes Hesse is one of a small group of genera characteristic of South Africa; there are related forms in the southwestern United States.

Length: 5 to 6 mm., of wing 4 to 5 mm.

As I have not been able to see or obtain material of *Pteraulacodes* Hesse, I quote Hesse's description of the genus:

Body similarly shaped; abdomen in males also cylindrical and in females conically pointed, also predominantly black, but with the sides of abdomen, hind margins of sternites, the femora and the tibiae yellowish or yellowish reddish to a variable extent. Vestiture with the erect hairs on body less developed, relatively sparser and shorter; hair on frons distinctly shorter and

sparser; that on face for the greater part wanting, present only as a conspicuous brush-like tuft anteriorly and overhanging apex of buccal cavity; that on disc of thorax very much shorter, finer and sparser; vestiture on mesopleuron also sparser and shorter, composed of scales and bristly hairs, greater part of pleurae even barer than in *Pteraulax* Bezzi; metanotal tuft also wanting; prealar, postalar and scutellar bristles however similarly developed, but apparently fewer in number; hair on abdomen, excepting only dense brush on sides of tergite 1, also sparse; transversely arranged bristly hairs across hind margins of tergites short, not developed to the same extent as in *Pteraulax* Bezzi, conspicuous and longish only on last tergite in males; scaling slightly more developed and denser than in *Pteraulax* Bezzi, very dense on frons and face, mostly lanceolate in shape, finer on body above; that on pleuron, mesopleuron, sternopleuron, hind margin of metapleural part and on coxae dense and cretaceous whitish; that on venter also very dense and that on legs as in *Pteraulax* Bezzi.

The wings have the membrane also wrinkled; basal comb wanting; three submarginal cells present; first posterior cell however open apically, not acute and closed as in *Pteraulax* Bezzi; squamae much smaller, more normal. Head large, subglobular, broader than thorax; eyes large, indented in hind margin and also with a short bisecting line extending from indentation, also in contact for some distance in front of ocellar tubercle in males, separated on vertex in females; occiput like that of *Pteraulax* Bezzi, the medial sulcus tending to be narrower; frons also convex in males and anteriorly in females; face from side however distinctly subconically prominent or snout-like, not gradually sloping into buccal cavity as in *Pteraulax* Bezzi, but overhanging the buccal cavity, the brush-like tuft of hair emphasizing this character; buccal cavity deep; genae very narrow and linear, the genal furrows not so distinct as in *Pteraulax* Bezzi; antennae with joint 1 relatively much shorter, cup-like and with much fewer and sparser hairs; joint 3 conical, gradually broadened basally, ending apically in a slender joint-like terminal joint bearing a relatively long style; proboscis confined to buccal cavity or only projecting slightly beyond buccal cavity; palps slender, longish, biarticulate, the apical joint clavate and very much shorter than basal joint.

The legs without any dense fine or longish hairs on front and middle femora below; middle and hind femora also with slender bristle-like spines below as in *Pteraulax*, those near base on hind femora also long and slender and more or less disposed irregularly in pairs, in males especially; tibiae also with the spicules on outer part long and bristly-like, and with the 2 or 3 lower spurs on middle and hind ones also markedly long and slender; claws with their apices bent downwards and the pulvilli well developed. Genital brush in females also terminal. Apical angles of last sternite in males slightly produced, more lobe-like and not rectangular as in *Pteraulax* Bezzi. Hypopygium of male very much like that of *Pteraulax* Bezzi; dorsal parts of basal parts also finely and relatively poorly covered with hair; beaked apical joints compressed, curved and elongate; a ventral aedeagal process in the form of a rod-like process also present; apex of aedeagus also ending in a transverse slit-like aperture in aedeagal process; lateral struts broadish, shoe-horn-shaped; basal strut with triangular lateral extension on each side basally and with its apical margin along dorsal aspect also with a lateral ledge-like extension.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of male very much like that of *Pteraulax*; dorsal parts of basal parts also finely and relatively poorly covered with hairs; beaked apical joints compressed, curved and elongate; a ventral aedeagal process in the form of a rod-like process also present; apex of aedeagus also ending in a transverse slit-like aperture in aedeagal process; lateral struts broadish, shoe-horn-shaped; basal strut with a triangular

lateral extension on each side basally and with its apical margin along dorsal aspect also with a lateral ledge-like extension.

Material available for study: None. I have not been able to personally examine these flies as they are known only from the unique types.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Pteraulacodes karoensis* Hesse, 1956.

Genus *Prorostoma* Hesse

FIGURES 130, 389, 622, 640

Prorostoma Hesse, Ann. South African Mus., Pt. II, vol. 35, p. 121, 1956a. Type of genus: *Plesiocera integra* Bezzi, 1922a, by original designation.

Small flies which in shape and length of abdomen and vestiture strongly resemble *Epacmoides* Hesse. The wing is essentially the same also; it is hyaline, the second vein arises abruptly in nearly the same position, the anal cell is open, the marginal cell has a more conspicuous kink subapically, and the end portion of this cell is a little more conspicuously swollen downward. The antennae are similar but whereas *Epacmoides* Hesse has a rather sharply triangular face, *Prorostoma* Hesse has the produced face rounded.

In comparison with *Epacmoides* Hesse, *Prorostoma* Hesse has the hind margin of the eye only slightly indented and emarginate; the scutellar margin is normally rounded and not slightly bidentate or bimammiform as in *Epacmoides* Hesse. Hesse contrasts this genus with *Epacmoides* Hesse in his key couplets; he states further that *Epacmoides* Hesse is almost without tiny bristles beneath the femora, but that they are numerous in *Prorostoma* Hesse; in *Prorostoma* Hesse I find 4 beneath the anterior femur, 5 beneath the middle femur and 5 below the hind femur (none in the female before me); Hesse states that there is double row: all of these bristles are minute, however.

Prorostoma Hesse appears to be a weakly characterized monotypic genus from South Africa.

Length: 4 to 9.5 mm.; wing, 4 to 8.5 mm.

Head, lateral aspect: The head is subglobular, the occiput moderately prominent above, and bears dense, short, erect pile extending almost to the eye margin. Only the outer row of hairs is curved forward; it is more extensively appressed at the indentation of the eye. Whole surface of the occiput pollinose or appressed micropubescent. The fringe along the inner occipital recess is rather dense. Eyes with a shallow indentation near the middle. Front densely pale pollinose, with abundant, fine, bristly pile obliquely and slightly curved forward and covering the whole front. Front very slightly convex. The face is prominent, but is bluntly rounded and does not extend as far as the apex of the antennae. In both of these respects it differs from *Coryprosopa* Hesse. Moreover, the surface of the face is pollinose with dense, short, appressed, stiff pile.

The proboscis is short, and rather stout, not longer than the oragenal recess, in which it is usually tucked away, and the labellum quite long, fully as long as the proboscis and with microspinulose surface. The palpus appears to consist of a short, basal segment that bears 1 or 2 long, slender bristly hairs and of a more flattened, moderately lengthened, apically blunt, micropubescent segment carrying 4 long, lateral, slender bristles and 2 or 3 at the apex. Its total length is about one-third the length of the proboscis. Antennae are small; the first segment is wide, short, distinctly wider than long, black with a thin, pale, apical rim of somewhat more extensive and extended cuplike appearance on the medial side. Second segment shorter than wide, distinctly convex and rounded on each side, nearly as wide as the first segment but broadly attached laterally, hence the entire antennae are strongly divergent. The third segment is pyriform, bulblike on the basal half, the thick, apical process somewhat asymmetrical, its outer margin plane, except near the base, the inner margin distinctly concave. The third segment bears a short, cylindrical microsegment no longer than wide with minute, concealed spine. The second segment laterally bears several long, stiff bristly hairs and a few fine, short hairs medially. Also, the first segment has a few short setae medially and dorsally and a tuft of somewhat longer hairs ventrally.

Head, anterior aspect: The head is circular, wider than the thorax, the eyes widely separated in the male by slightly more than the thickness of the first antennal segment and the ocellar tubercle in the male is quite prominent with vertical sides; the ocelli set in a nearly equilateral triangle. In the female the ocellar tubercle is a little less prominent and the vertex is almost as wide as the front, the sides of the front and vertex being only slightly convergent. Moreover, the upper part of the front in the female, immediately in front of the ocellar tubercle, is rather strongly and medially depressed or sunken, and distinctly concave. This wide fovea is characteristic. The antennae are separated at the base, though rather narrowly. The first two antennal segments touch apically and medially due to the medial extension of the first segment. The oragenal cup is distinctly ventral in position, at most very slightly oblique. It is elongate oval, rather deep, slightly pinched in the middle, and this is the only point at which the inner walls are vertical. Both below and above the inner walls are rather strongly sloping. The gena is quite linear, the only deep depression is a short one between the eye and the oragenal cup at the point where it is compressed inward. Here there is a moderately deep tentorial fissure. The sides of the face are not only densely pollinose but bear numerous, stiff, bristly hairs curled downward and forming a fringe that extends along the edge of the whole upper half of the oragenal cup. From the posterior aspect the lobes of the occiput are in contact, except that there is behind the vertex between the posterior eye corners a deep,

continuous, triangular, vertical shaft or pocket, which appears to extend through to the occipital cavity.

Thorax: The thorax is black, the mesonotum low and gently convex, covered loosely with abundant, coarse, suberect, shining yellow pile, in places rather matted and more appressed on the posterior half of the mesonotum. Notopleural and humeral pile more tangled and erect and longer. Anterior mesonotal collar of pile long. Notopleuron with 2 stout, pale bristles. Postalar callosity with 2 long, slender bristles. Scutellum more shining than the mesonotum, especially on the apex, the disc faintly pollinose and covered with pile similar to that of the mesonotum. There are a few fine, long, but not conspicuous hairs across the mesonotum and in front of the scutellum. Scutellar margin with 2 or 3 pairs of slender bristles. Propleuron with erect, vertical fringe of long hairs. Whole pleuron silvery gray pollinose. Mesopleuron almost entirely covered with coarse, flattened, subappressed hairs which are tangled above and with longer, bristly hairs on the posterior half. A very large triangular area of the sternopleuron bears matted, appressed, scaliform pile with, at the extreme ventral part a fringe of bristles in one row. Pteropleuron and hypopleuron bare. Lateral metanotum and anterior metapleuron each with a rather conspicuous tuft of coarse, partly erect, partly appressed or curled hairs. There is no patch of pile behind the spiracle. Squama short with a short, thin fringe of pile.

Legs: The legs are rather slender and comparatively short. Anterior femur gradually thickened a little toward the base; middle femur likewise somewhat stouter in the middle and toward the base. Hind femur stout, anterior femur with 4 or 5 stout spicules ventrally, middle femur with 10 anteroventrally and 7, a little longer, posteroventrally, also with some spines on the lower, inner aspect of the hind femur. Anterior tibia much shorter than the middle pair; slender, with appressed pile and with 6 or 7 minute, fine, suberect setae dorsally in each of 2 rows and 7 or 8 setae posteroventrally. Middle tibia with equally fine, slender, oblique, bristly setae, 3 or 4 anteroventrally, 5 or 6 on each side dorsally and 7 or 8 posteroventrally. Apical spines long and stout. Hind tibia not longer than the middle pair, only slightly thicker with 4 or 5 setae in each dorsal row, 4 ventrolaterally and 6 weaker ones ventromedially. Apex with one spinous bristle much longer than the others. Tarsi short, slender, sharp, strongly curved at the apex, pulvilli long.

Wings: The wings are hyaline, long and slender and villose. The auxiliary cell yellow. Second vein with a strong bend anteriorly before the apex. End of marginal cell broadly rounded backward. The anterior branch of the third vein arises abruptly but is rounded at the bend and curves forward near the middle. First posterior cell long and slender, a little narrowed at the apex, the anal cell equally widely open. The anterior crossvein enters the discal cell before the middle; the second vein arises abruptly but not quite rectangularly and has a rounded bend without spur. It arises a little

before the midpoint between the beginning of the discal cell and the anterior crossvein. Ambient vein complete. Alula well developed. Costa with a lappetlike spur.

Abdomen: In the male the abdomen is elongate and subcylindrical, slightly longer than the thorax, dully shining and thinly pollinose, the pile is rather dense, brownish yellow, partly flat-appressed with a few, scattered, long, fine hairs arising posteriorly along the outer part of the tergites, especially the first four. Sides of the first tergite with dense, broad band of coarse, erect, pale pile. The fringe of long, fine, erect hairs along the outer margins of the anterior tergites, while consisting of only scattered hairs, is conspicuous. I find 9 tergites in the male, the ninth quite short, the tenth larger, slanted downward and forming a curled hood enclosing the remainder of the genitalia. The female abdomen is slenderly oval. At the end of the third segment a little wider than the thorax and densely covered with flat appressed, long, brownish yellow, scalelike pile. I find 7 well-developed tergites in the female and a very short eighth tucked under the seventh. In males the basimeres are large and lie close together ventrally.

Dr. A. J. Hesse sums up the hypopygium of these flies in the following words:

Hypopygium of males with the apical angles of the opposing last sternite also slightly angularly prominent; basal parts of hypopygium also divided into two parts by an impressed suture, each covered dorsally with shortish hair, the base of each produced into a lobe-like process and the apical neck-like part narrow and well marked off from basal two-thirds, the outer apical angle not prominently produced as in *Plesiocera*; beaked apical joints elongate, curved outwards near apex, without any distinct or visible hairs above; aedeagus shortish apically, passing basally and on dorsal aspect into a broadish flattened process on each side, with the lateral ramus on each side from each basal part fused together bandwise, across aedeagal complex, to form a ventral aedeagal process, prolonged on each side into a ventrally directed process the apical part of which is flattened and broadened.

Material available for study: A pair of the type-species sent to me through the courtesy of Dr. A. J. Hesse.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no comment upon the behavior of adults.

Distribution: Ethiopian: *Prorostoma integrum* (Bezzi), 1922 (as *Plesiocera*).

Genus *Coryprosopa* Hesse

FIGURES 132, 386, 632, 647

Coryprosopa Hesse, Ann. South African Mus., vol. 35, p. 118, 1956. Type of genus: *Coryprosopa lineata* Hesse, 1956, by original designation.

Small flies superficially appearing like *Aphobantus* Loew, with elongate tapered abdomen, a little compressed and subcylindrical in the male and with blunt apex, but rather quickly recognized by the long, scattered, coarse, bristly hairs arising from the posterior

half or more of the tergites and the posterior borders on the female, and similar shining mesonotal hairs, again more conspicuous in the male. Whole surface everywhere pollinose, the general coloration primarily pale, with black stripes on the abdomen and the mesonotum centrally blackish, and both of these areas with opaque, matted, pale, scaliform pile.

In addition, in this genus, the face is extremely prominent and conically extended beyond the pyriform, bulbous, third antennal segment. Moreover, the chiefly hyaline wings mostly tinted in the costal and auxiliary cells; it is noteworthy for the rectangular origin of the second vein with basal stump and for the anterior bend in the second vein on the outer fourth of this vein. Finally, the lobes of the occiput are separated.

Coryprosopa Hesse is a monotypic South African genus related to *Plesiocera* Macquart, and *Conomyza* Hesse from which it is distinguished by the above characters.

Length: 5.5 to 9 mm.; wing 4.5 to 6.5 mm.

Head, lateral aspect: The head is subglobular, with the occiput only moderately extensive above in either sex, and from the lateral aspect very little indeed shows from the lower half. Middle of the eye margin shallowly indented. The front is rather flattened, the vertex sinking below the eye margins. Whole front and face pale yellow and densely pale pollinose, the pile in the male consists of 2 or 3 rows of slender, pale, bristly hairs directed forward. In the female the pile is darker, more nearly erect and more irregular. The pile of the occiput is fine and short and appressed outward. Inner margin of the occiput with a scanty fringe around the circular recess. The face in *Coryprosopa* Hesse is very characteristically extended forward into a long, beak-like, triangular cone, nearly equilateral and reaching beyond the apex of the antennae. The proboscis is short, comparatively stout with flattened, pointed labellum; while Hesse (1956) notes the labellum is nearly half as long as the rest of the proboscis, it appears to me to be a little less than one-third as long. And in the material before me the proboscis is tucked in the oral recess lying flat against the head. Labella surface spinulose. The palpus is quite long and slender, cylindrical, curved, with a few fine, long, erect, bristly hairs at the base. It appears to have a short, second apical segment.

The antennae are small and short, the first segment is short and quite wide, scarcely half as long as its width viewed from above. The second segment is less wide, only half as long as the first segment and this segment is also only half as long as wide. The third segment is pyriform but somewhat asymmetrical, the basal bulb-like portion is attached somewhat broadly and medially on the second segment, bulging out medially to a moderate extent and only gradually tapering to the blunt apex which bears a short, spine-tipped microsegment. This segment is covered with pale scalelike micro-pubesence. The second segment has a fringe of bristly setae, except medially. The first segment has a tuft of shining, scaliform pile laterally, and it has also a

shelving, more or less cuplike ledge developed medio-apically, and touching the ledge of the opposite antennae.

Head, anterior aspect: The head is circular and distinctly wider than the thorax. Eyes of the male strongly separated by a distance equal the breadth of the first antennal segment. Eyes more widely separated in the female. The vertex is scarcely narrowed over the front, and it is at least 3 times as wide as the space between the outer edges of the ocelli. The antennae are widely separated, although the first two segments touch at the apex, usually, because of the lobelike outgrowth of this segment. Because of the position of the second and third segments the outer part of the antennae is strongly divergent. The ocellar tubercle is equilateral, rather convex and prominent, especially in the male. The oragenal recess is set low upon the head and is slightly oblique, hence it is readily inspected only from the bottom. The face is very strongly conically projected forward. The gena is a mere linear strip along the eye margin and there is a paper-thin, tentorial fissure near the bottom of the eye. The face is pale pollinose with scattered, fine, pale bristles in the male and rather stiffer, stouter, reddish bristles in the female. From the posterior aspect the occiput is bilobate, deeply cupulate and dorsally the lobes fail to meet by the distance between the ocelli.

Thorax: The thorax is longer than wide, the mesonotum densely pollinose and also densely covered with matted, flat-appressed, coarse pile. Anterior mesonotal fringe of erect pile short and scanty. Humeri rather inflated, pale yellow, and pollinose and with an extensive tuft of long, coarse, somewhat flattened hairs. Notopleuron with scattered, slender bristles and in the posterior corner with 2 very stout, long, pale bristles. Postalar callosity with a few slender bristles, prescutellar margin with a row of bristles and the scutellar margin with 5 or 6 pairs of bristles. The surface of the scutellum has flat-appressed, coarse, long pile. Middle of mesonotum blackish in ground color but yellow in front of the scutellum and yellow throughout the entire lateral margins. Scutellum yellow, except for a medial, blackish stripe. Pleuron yellow and pollinose, mesopleuron with only scanty, scattered, long hairs and a few others on the sternopleuron. Pteropleuron and hypopleuron without pile. There is a tuft of hairs on the metapleuron in front of the halteres and the lateral metanotum bears a large, bushy tuft of coarse, erect pile. Halteres small, squama short with a fine, short fringe in one row only. All the thoracic pile is shining where erect but rather opaque where flat-appressed.

Legs: The legs are yellow. The femora rather stout, especially the hind pair. Anterior femora much shorter than the middle pair and the last two pairs nearly equal in length. All the femora covered rather loosely with large, flat-appressed, yellow scales. Anterior femur with 7 or 8 minute, erect, black setae ventrally on the swollen black half or more. Middle femur with very fine, short, erect bristles, 6 anteroventrally, 3 posterior

ones. Hind femur with fine, erect bristles that are a little more stout and also short. There are 6 antero-ventral, 2 ventromedial ones apically, a dorsal bristle on each side at the apex and 1 or 2 other dorsal bristles near the apex. Anterior tibia short and quite slender, much shorter than the others; this tibia has an antero-dorsal row of about 10 minute setae and 3 others equally minute posteriorly. Middle tibia with fine, short, oblique, slightly longer, scarcely more stout. This hind tibia has 4 rows of bristles, 6 anteroventral, 8 antero-dorsal, 10 or more dorsomedial, and 3 or 4 ventromedial. Apical spur longer, sharp and stouter than the other bristles of the tibiae. Tarsi short, claws strongly curved at the apex and fine and sharp at the apex. The pulvilli are slender, but extend to the apex of the claws.

Wings: The wings are hyaline, vitreous with iridescent tints and the whole wing is elongate and slender. The costal and auxiliary cell are entirely brownish yellow and this yellow continues opposite the base of the discal cell as far as the third vein and includes the third vein. There are 4 diffuse, brownish spots, one just before the origin of the third vein, one at the lower end of the second basal cell, one over the basal end of the first submarginal cell, and one over the anterior crossvein. These seem to be best developed in the female, males may lack them or may have them much reduced. There are 2 submarginal cells, the second vein is rather strongly bent subapically, the marginal cell is rounded apically below. The second vein arises rectangularly with basal spur and its origin lies about halfway between the base of the discal cell and the anterior crossvein. All 4 posterior cells are open, the first one a little narrowed, and the anal cell is as widely open as the first posterior cell. Axillary lobe narrow, ambient vein complete, alula quite short, costa with a stout basal swelling and weak comb of bristles. There appears to be a bulbose thickening in the first basal cell below where the radial sector begins. Anterior crossvein enters the discal cell in the middle.

Abdomen: The abdomen is elongate, about $1\frac{1}{2}$ times as long as the thorax, subcylindrical, a little compressed in the middle on each side, brownish orange or brownish yellow, opaque yellow pollinose. There is a black vittae on each side originating in a rather large, subquadrate, blackish spot on each side of the second segment in both males and females, and slightly narrowing and fading away on the seventh tergite. I find 7 well-developed tergites in the female with 2 minute, additional ones beyond. Males with 7 tergites, each of nearly equal length and with 2 other shorter ones slanting downward; the male terminalia are distinctly recessed within these and a little more exposed below. Pile of the male abdomen dense, opaque yellow, flat-appressed, rather coarse and flattened but also with a rather conspicuous, loose, irregular band or double band of long, slender, shining yellow bristles or bristly hairs curled backward from along the posterior margins of the tergites. Female abdomen with more scanty, appressed pile that seems to be finer in character and also with scattered,

long, fine hairs along the posterior margins of the tergites.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium of male not so exposed as in *Plesiocera*, withdrawn into apical part of abdomen; last opposing abdominal sternite relatively shorter than in latter genus, its apical angles also slightly pointed and subprominent; basal parts of hypopygium itself divided into two parts by a dorsal dividing suture, each part with a basal tongue-like lobe and apical angle of each basal part not produced to the same extent as in *Plesiocera*; beaked apical joints entirely different, broadened in basal half, produced apically into a outwardly curved beak, the outer apical angle angular, the dorsum covered with hairs, especially towards base; aedeagus with the apical part shortish, produced basally on dorsal aspect into a prominent process on each side, the lateral ramus on each side from each basal part coalescing and forming an elongate ventral process, the ventral part of which is hollowed out and the apex slightly recurved; lateral struts very well developed, more strongly developed than in *Plesiocera*; basal strut also longer and broader.

Material available for study: A pair of type-species sent by Dr. A. J. Hesse for dissection and study.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no comment on the behavior of adults.

Distribution: Ethiopian: *Coryprosopa lineata* Hesse, 1956.

Genus *Epacmoides* Hesse

FIGURES 129, 380, 646, 650

Epacmoides Hesse, Ann. South African Mus., Part II, vol. 35, p. 125, 1956. Type of genus: *Plesiocera blumbonatum* Bezzi, 1922, by original designation.

Hesse (1956), pp. 127-128, key to 4 Ethiopian species.

Small flies with short, appressed pile, except on the sternites, mesopleuron, and anterior margin of the mesonotum. The abdomen is as long as the thorax, the scutellum included, but in males is rapidly narrowed to a cylindroid form beyond the second segment; females elongate oval with the last segment triangular. The wings are hyaline, and these flies are readily distinguished from *Aphobantus* Loew, which they resemble in general aspect, by the formation of the second vein; this vein arises abruptly from the third vein at a point a little beyond the middle of the space between the base of the discal cell and the anterior crossvein. The face is triangularly produced and in this respect resembles *Epacmus* Osten Sacken from which it is again readily separated by the abrupt origin of the second vein. Moreover, it should be noted that in addition to rather strong bristles on the margin of the scutellum there is a transverse row of equally well-developed bristles lying in front of the scutellum. Notopleuron also with similar bristles and anterior mesonotal margin with a collar of pile.

The metanotum and upper and posterior metapleuron have much coarse tufted or partly appressed pile. Proboscis limited to the oragenal recess.

The anterior branch of the third vein is strongly sigmoid, the end of the marginal cell ovably rounded and swollen downward.

This small genus contains only 4 South African species.

Length: 3.6 to 8 mm.; of wing 4 to 8 mm.

Head, lateral aspect: The head is subglobular, occiput only moderately developed and with rather dense, appressed, scaliform pile reaching to and making a matted fringe along the upper half of the eye margin; it begins at the indentation of the eye, which is deeper and more conspicuous than in *Prorostoma* Hesse. Inner margin of the occiput with a very scanty fringe of scattered hairs. The front is flat on the upper half below the ocelli but is distinctly swollen in the male in *Epacmoides* Hesse, much more so than in *Prorostoma* Hesse. Also the entire front, except immediately anterior to the ocelli, is shining and bare of pollen, whereas in *Prorostoma* Hesse the front and vertex are uniformly and densely silvery pollinose. The pile of the male front is rather dense, bristly, and projected forward. The face is triangularly produced almost as far as the apex of the antennae, it is more pointed and acute than in *Prorostoma* Hesse and bears scattered, appressed scales, the surface polished. The proboscis is slender with a short, flattened, oval, somewhat pointed labellum. It is shorter or in any case not longer than the oral recess. Palpus rather long and slender with a few long hairs near the apex and laterally in the middle, and apparently with a short basal segment. It is about one-third as long as the proboscis. The antennae are similar to *Prorostoma* Hesse, the first segment flared and widening both medially and apically with apical fringe of stiff bristly hairs longer laterally. Second segment quite short, less than half as long as wide, the third segment smaller, bulblike at the base with a long slender, cylindrical process, not quite twice as long as the basal part.

Head, anterior aspect: The head is circular and a little wider than the thorax. The eyes are separated in the male by a distance equal the apical width of the first antennal segment. The vertex is sunken beneath the eye margin, the ocellar tubercle prominent with vertical sides and very large, wide, anterior ocellus. The ocelli lie in an equilateral triangle and there is a row of coarse, bristly hairs extending forward over the middle of the ocellar tubercle. Pile of anterior front distinctly scaliform. In the female the eyes are much more widely separated and the sides of the front converge only slightly. The ocellar tubercle is equally prominent, likewise with vertical sides and from the anterior ocellus to the middle of the front there is a marked, concave depression or concavity. While the antennae are rather widely separated at the base, nevertheless the first segments touch medially and apically. The oragenal cavity is quite deep, elongate, with vertical sides and slightly pinched in along the middle. The genae are quite linear along the middle of the oragenal cavity and are slightly wider below. Viewed from

behind the occiput is bilobate and very different from *Prorostoma* Hesse. Where the lobes touch in *Prorostoma* Hesse with a deep triangular recess, the lobes in this genus touch but lack any deep anterior pocket.

Thorax: The thorax is short and black, the mesonotum is low, a little convex, rather higher than in *Prorostoma* Hesse. It is loosely covered with coarse, flat appressed, scaliform pile. The anterior collar is rather high, and narrow, the coarse bristly hairs rather long and the flat appressed pile begins immediately behind the collar. Humerus with a dense, tangled tuft of erect and partly appressed pile. Notopleuron densely pilose and with a large, loose clump of 8 or 9 slender, red bristles, 2 of them more stout. Postalar callosity with at least 3 long, slender, red bristles, and there is a band of similar bristles in front of the scutellum which are curved backward. Scutellum black, with matted, appressed pile on the disc and the lateral corners, and in the medial fovea on the posterior margin of the scutellum. Scutellum is rather thick apically, polished black, rather strongly bimammillate. The margin has 4 or 5 pairs of long, red bristles. Pleuron pollinose, whole mesopleuron and almost the entire sternopleuron with dense mat of flat-appressed, scaliform pile. The upper and posterior mesopleuron have a few long, erect, bristly hairs. Propleuron with a narrow, long fringe. Metanotum and the anterior metapleuron in front of the spiracle and an equally conspicuous patch behind the spiracle made up of flat-appressed, scaliform pile. However, that on the metanotum is more erect. Halteres short but the knob large and short. Squama short with a weak fringe.

Legs: Anterior and middle femora distinctly but not strongly thickened over the middle and more so at the base. Hind femur stout but not swollen. All femora covered with dense, yellowish white, large, flat-appressed scales. Middle femur with 2 quite stout, anteroventral bristles and 2 or 3 minute setae posteriorly. Hind femur with 5 bristles ventrolaterally on the apical half, 3 of them stout; 1 stout bristle and 2 or 3 smaller ones dorsolaterally near the apex. Anterior tibia with fine, bristly spicules, 3 extremely minute spicules dorsally, 5 which are a little longer posteriorly, and 5 still larger ones posteriorly ventrally. Middle tibia with only minute bristles dorsally, but with 5 stouter, longer bristles ventrally. Hind tibia with 4 rows of bristles, the anteroventral row contains 4 moderately long, stout bristles, the 2 dorsal rows contain 5 or 6 quite small bristles and the ventromedial row contains 6 slender bristles. Tarsi slender, short, but rather strongly spiculate below. Claws slender, only slightly curved with the pulvilli rather long.

Wings: The wings are hyaline, elongate, but comparatively broad, wholly villose. Auxiliary cell yellowish. Second vein with a strong, preapical bend forward so that the marginal cell is rounded outward posteriorly. The anterior branch of the third vein rises abruptly, not quite rectangularly and makes a rounded, strong bend outwardly and then is bent forward a little

beyond the middle so that the second submarginal cell has nearly or quite parallel sides on both its basal half and its outer half. First posterior cell open widely, the anal cell opened half as wide. The anterior crossvein enters the discal cell a little before the middle. The second vein arises abruptly, has a rounded bend, its point of origin is halfway from the beginning of the discal cell to the anterior crossvein. Ambient vein complete, alula rather wide. Costa at the base thickened, and with a large lappetlike spur.

Abdomen: The abdomen in the male is short, scarcely as long as the thorax, gradually narrowed beyond the base of the second segment, subcylindrical, slightly compressed laterally and apically and densely covered with flat-appressed, pale scales and scaliform pile and each tergite with a subapical fringe of fine, bristly, reddish hairs, of no great length and appressed backward. Color of abdomen black with the posterior margins obscurely and rather widely reddish brown. Middle of the first segment with on each side of the midline a large, more or less semicircular tuft of flat-appressed, yellow scales, the outer third of this segment with dense band of long, coarse, erect, spikelike pile. Extreme lower margins of the second, third and fourth tergites with considerable, long, erect, coarse pile. Female abdomen elongate conical with slightly rounded sides and gently convex on the disc. It is densely covered with matted, appressed, scaliform pile partly yellowish or reddish brown, especially on each side of the middle and on the posterior part leaving a distinct, medial, pale yellow stripe and a less distinct row of disjointed spots laterally. I find 7 well-developed tergites, the last one is compressed laterally and has a heavy fringe of bristly hairs surrounding the female terminalia. I find 7 well-developed tergites in the male and a short eighth turned downward and almost concealed beneath the seventh. It encloses the small genitalia, the two pieces of which lie side by side recessed and turned to one side.

Since Dr. A. J. Hesse was able to base his conclusions upon a greater number of species, I quote his remarks upon the male hypopygium:

Hypopygium of males with the lateral apical angles of opposing last sternite also somewhat angular; basal parts of hypopygium itself differing from that of *Prorostoma* in not having the apical part so well marked off; beaked apical joints more like those of *Coryprosope*, not narrowish throughout, but with an outer angular apical part; aedeagus without a complex, ventral, aedeagal process, the process, if present, in form of a forwardly projecting ledge or a pair of stylets; basal strut sometimes with a distinct, shelf-like, lateral ledge present on each side.

Material studied: A pair of the type-species sent by Dr. A. J. Hesse to me.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no comment on the behavior of adults.

Distribution: Ethiopian: *Epacmoides albifrons* Hesse, 1956, *albifrons pallidulum* Hesse, 1956; *biumbonatum* (Bezzi), 1922 (as *Plesiocera*); *cryptochaunum* Hesse, 1956; *xerophilum* Hesse, 1956.

Genus *Stomylomyia* Bigot

FIGURES 131, 385

Stomylomyia Bigot, Bull. Soc. Ent. France, ser. 6, vol. 7, p. xxxi, 1887a. Type of genus: *Tomomyza europaea* Loew, 1869, as *Stomylomyia leonina* Bigot, 1887, by monotypy.

Small, comparatively slender flies, varying from yellowish brown to blackish in ground color with some brownish or yellowish or rarely silver gray pollen, and also with scattered, slightly flattened pile or even narrow scales in some species. They are rather readily recognized by the sharp and conically produced face and the clear, hyaline wings, which may be tinged with brown or yellow near base and costa. Also, note the origin of the second vein which is abrupt and rounded, and lying halfway between anterior crossvein and base of radial sector.

All of the species of this genus have 3 submarginal cells, separating them at once from *Plesiocera* Macquart which also has a much less sharply produced face. Engel (1934) made *Stomylomyia* Bigot a subgenus of *Plesiocera* Macquart placing 5 species within it. I have had for study the type-species of *Stomylomyia* Bigot, received through the courtesy of the British Museum, and I have been able to study the type of *Exepacmus nasalis* Melander. Dr. A. J. Hesse kindly sent several South African species of *Plesiocera* Macquart for study, and I have the type-species as well. *Stomylomyia* Bigot is distinguished from *Plesiocera* Macquart by the oblique, basal origin of the second vein; its face is long and conical extending well beyond the antennae. It is separated from *Exepacmus* Coquillett by the deep, conspicuous indentation of the posterior eye margin. All of these small genera have a general similarity in appearance, and *Desmatoneura* Williston belongs in the same group, differing, as does *Plesiocera* Macquart, in having only 2 submarginal cells and distinctions; however, it is worth noting that the peculiar front found in *Desmatoneura* Williston is matched by the front of *Plesiocera flavifrons* Becker (Engel 1934, fig. 159); the latter species differs sharply in facial ledge and indentation of the eye.

As now formed, *Stomylomyia* Bigot is restricted to Asia Minor and southern Europe and North Africa.

Length: 3.5 to 11 mm.; **wing** 3.0 to 9 mm.

Head, lateral aspect: The head is subglobular, the occiput is short above and below. There is a very shallow indentation at the middle of the posterior eye margin without accompanying notch, hence this genus is difficult to separate from the Cylleninae. The pile of the occiput consists of erect, micropubescent and a fine, scanty fringe along the sides of the interior occipital cup and the pile becomes a little longer and more conspicuous dorsally behind the vertex on each occipital lobe. The front is short but distinctly protuberant above the antennae. The pile is loose, scanty, bristly, of no great length and scattered over the whole of the front. The ground color is shining black with some

pollenlike micropubescence down the middle of the front, linearly along each eye margin and just above the antennae. The face in profile is strongly and conically peaked forward. In this respect it is somewhat like *Coryprosopa* Hesse, from which it differs in the presence of 3 submarginal cells. The face is bare and shining, the conical part, which represents an extension of the oragenal cup, is sharply delimited from the rest of the face by a narrow, almost rectangular crease. Face with scanty micropubescence laterally, and a few short, bristly hairs below on the edge of the peak of the oragenal recess. The eye is only moderately large, distinctly long on the upper half, the upper facets are a little enlarged.

The proboscis is slender, not longer than the oragenal recess, and the labellum slender, rather flattened, and nearly one-third the total length of the proboscis. The palpus is quite long and slender and almost filiform. I can only find one segment; it bears a few, fine hairs laterally. The antennae are attached near the upper third of the head, the first two segments are subequal in length and both are short. Viewed from below the second segment is a little longer than the first. Ventrally the occiput descends rather strongly beneath the eye, so that the genal region is extensive at the bottom of the head, though very short and linear above.

Head, anterior aspect: The head is circular and much wider than the thorax. The front in the female is widely separated by a distance somewhat greater than the space across the first antennal segment measured from the outside. The ocellar tubercle is slightly obtuse, large, low, a little flattened. The antennae are narrowly separated by the width of the first segment in the female. The oragenal recess is unusually long, quite deep throughout, and strongly narrowed anteriorly. The crease separating the sides of the oragenal recess from the gena is distinct and rather deep. The gena is narrow, except below the eyes where it is extensive. The ventral occiput extends even deeper below the eyes. From the posterior view the occipital lobes are broadly, gently rounded, widely separated, deep, and divided by a rather wide fissure.

Thorax: The thorax is rather convex though not conspicuously so. Mesonotum and scutellum are blackish with brownish yellow pollen and scanty, more or less appressed setate pile dorsally and a considerable amount of narrow, appressed scales which are more numerous along the anterior margin of the mesonotum, above the wing, on the notopleuron and humerus. The upper mesopleuron bears in addition some appressed scales, and bears a patch of long, scattered, bristly hairs dorsally. There are a few, appressed scales on the lower mesopleuron and upper sternopleuron and there is a collar of scanty, erect pile along the anterior margin of the mesonotum. There are 2 moderately stout, long, curved, red bristles on the notopleuron and 4 pairs of long, more slender red bristles on the margin of the scutellum. Pteropleuron, hypopleuron, and the metapleuron, with the exception of the metanotum, bare and

pollinose only. The metanotum bears an extensive, conspicuous tuft or clump of long, erect scaliform pile and in this respect is like *Coryprosopa* Hesse. There is also a radiating tuft of appressed scales behind the spiracle and below the haltere. The squama is short.

Legs: The femora are loosely covered with scattered, flat appressed scales, the hind femur has 2 minute, slender bristles in the middle laterally, 2 others much longer and much thicker on the outer half. The anterior tibia bears some weak spicules, middle and hind femur with more distinct bristles, slender and oblique. On the hind femur there are 3 rows, each with 4 or 5 bristles.

Wings: The wings are hyaline and microvillose. The second vein arises abruptly but with rounded bend about halfway between the upper end of the second basal cell and the anterior crossvein. The anterior crossvein enters the discal cell at the middle. There are 3 submarginal cells. The anterior crossvein arises almost rectangularly as a plane, simulated crossvein and at the end of the crossvein it sends a backward spur to join the second vein, this spur vein represents the third branch of the radius. The apical part of the second vein and the anterior branch of the third vein both bend upward, ending before the apex of the wing. First posterior cell widely open, the anal cell also widely open. axillary lobe and alula both moderately narrow. Ambient vein complete.

Abdomen: The abdomen is elongate, about as long as the head and thorax together, subcylindrical, blackish, feebly shining, with thin pollen and with loose, scattered, moderately abundant, appressed scales, which are somewhat wider laterally, more narrow dorsally and there are wide, conspicuous scales on the sternites. Female terminalia with a dense fringe of hairs at the apex.

Material available for study: Material for the type-species in the collections of the British Museum (Natural History). Also the type of *Exepacmus nasalis* Melander. And for comparison with the related genus *Plesiocera* Macquart, the type-species given me by the British Museum (Natural History) and several South African species furnished through the generosity of Dr. A. J. Hesse.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic: *Stomylymyia europaea* (Loew), 1869 (as *Tomomyza*), *europaea aegyptiaca* Bezzi, 1925, *europaea nigritrostris* Bezzi, 1925 [= *leonina* (Bigot), 1887 (as *Stomylymyia*)].

Genus *Plesiocera* Macquart

FIGURES 125, 127, 381, 643, 648

Plesiocera Macquart, Diptères exotiques, vol. 2, pt. 1, p. 82, 1840.

Type of genus: *Plesiocera algira* Macquart, 1840, by monotypy.

Calledar, new subgenus. Type of subgenus: *Plesiocera psammophila* Hesse, 1956.

Engel (1934), p. 391, key to 7 Palaearctic species.

Hesse (1956), pp. 99-102, key to 7 species.

Medium-sized flies in the type-species, with tapered, nonconstricted abdomen, the ground color black with grayish-ochre pollen overlaid, thinner on the mesonotum and abdomen, more in evidence elsewhere. The pile is rather yellowish, nearly opaque and erect on the anterior third of the mesonotum and with much appressed brassy yellow pile upon the remainder of the mesonotum, scutellum, and abdomen; basal corners of abdomen with dense, conspicuous tuft of erect, golden pile. The face is projecting forward and separated by a distinct crease, sharper laterally, and crossing a short distance below the antenna. Marginal cell at end with a distinct, thumblike bend downward; wings largely hyaline, faintly brownish on foreborder, except at apex. The anal cell is widely open. The second vein arises opposite the base of the discal cell and at a gently acute angle, or sometimes a little more abruptly. The legs in the type-species are pale yellow; anterior tibia with only ultramicroscopic black microspinules; hind tibiae with distinct, regular, slender, black spines throughout. Claws and pulvilli small but well developed. In the type-species the posterior border of the eye is deeply indented and clearly bisected, and affinity appears to be with *Epacmus* Osten Sacken. I have only females.

Plesiocera Macquart contains one subgenus, *Calledar*, new subgenus, which is described herein.

Head, lateral aspect: The head is globular with the occiput very extensive dorsally but strongly rounded and sloping inward. The central fringe is long and dense, the cavity large and very deep. The entire outer surface of the occiput is pollinose and densely covered with short, nearly erect, golden pile which tends to curl forward. There is a tuft of longer, golden pile extending outward opposite the indentation of the eye. The front is convex due to the produced and greatly rounded head. It is scarcely visible above the eye profile, bears golden pollen and a mixture of fine, black and golden, erect hairs. The eye is reniform, the indentation deep and broad, the lower angle of the indentation more acute than the one above, and there is rather long, distinct, horizontal notch in the eye at the point of indentation.

The face is a little extended forward beneath the antennae but rounded and retreating to the point where the very extensive oragenal cup begins to jut out. This dorsal and lateral anterior wall of the oragenal cup is sharply demarcated from the face by a conspicuous, circular crease. Whole face and oragenal cup on the upper half is golden pollinose, and bears scattered, fine, more or less erect, black and yellow hairs, especially along the sides. This pile is not quite as long as the first antennal segment. The proboscis is slender, the labellum likewise, not longer than the oragenal recess into which it may be completely hidden when at rest. Palpus slender and small with a few fine, long, golden hairs. Antennae attached at the middle of the head. They are small, the first segment is the largest, 2 or 3 times as long as the second and this segment is strongly

widened medially toward the apex. It bears bushy, long, bristly pile laterally and below with shorter setae medially and dorsally. The second segment is wider than long and bears long, fine setae on all sides. Third segment basally as wide as the second segment, rounded at the base and progressively narrowed to the apex. The styler portion is thick and bears a distinct, cylindrical, spine-tipped microsegment. This third segment is about as long as the first two together, or slightly longer.

Head, anterior aspect: The head is circular and considerably wider than the thorax. Eyes in the male slightly separated, or by the width of the ocellar tubercle in Palaearctic species, or in Ethiopian species also separated by the breadth of the ocellar tubercle. In the female of the type-species the eyes are separated at the vertex by nearly 3 times the width of the small ocellar tubercle, which posteriorly and posterolaterally is very high, steep, and vertical. The width of the female eye is also equal to the length of the third antennal segment. In African species it varies, but it is usually little more than twice the width of the first segment. This first segment is not very wide at the base but expands considerably on the medial side toward the apex; remaining two segments are divergent, the second segment not more than half as long as the first, more narrow, shorter than wide and cylinder-like rather than bead-shaped. First segment with a few short setae above but with a conspicuous covering of fine, black bristles over the whole lateral surface which extends slightly beyond the second segment. There are shorter bristles below. Second segment with fine setae on all sides. Third segment more narrow than the second, plane at the base and nearly plane dorsally. Below, this segment rapidly narrows and tapers uniformly to the thick apex, which bears a distinct, short, spine-tipped microsegment.

The oragenal cup is rather wide, but about 3 times as long as its inner width. Anteriorly a short distance beneath the antennae the oragenal cup is very strongly produced. Both the upper margin of the produced portion and laterally the upper half are rounded and convex or bulging outward a little. It is sharply separated from the face by a deep crease and the height gradually diminishes until it is quite low just before the base of the proboscis. Since in the middle there is a slight diagonal, foveate depression, it would seem that this strong, jutting forward of the oral walls has an upper facial component and a posterogenal component. The tentorial fissure is a mere line but quite long, leaving a noticeable border along the lower eye which is pollinose, and contrasting because the oragenal cup is more thinly pollinose. Sides of both the pollinose face above and the sides of the whole anterior margin of the oragenal cup covered with long, scattered, bristly hairs. The head viewed from above shows the occipital lobes to be adjacent but with a deep furrow between and with a large, deep triangular pocket behind the vertex.

Thorax: The thorax is slightly longer than wide, the scutellum excepted, and also it is very slightly wider behind than in front. The mesonotum is low and slightly convex, black and rather densely olive-brown pollinose. The pile consists of dense, shining, brassy, appressed, slightly flattened hairs, which become more strongly appressed and more abundant and conspicuous on the posterior half of the mesonotum and likewise shorter but which anteriorly change to longer, more erect, dense pile merging into the anterior collar of long, dense, erect pile. The humerus is swollen and bears long pile like that of the anterior collar. Notopleuron with a clump of weak bristles, one of them longer and stouter than the others. Upper postalar callosity with bristly pile and 7 or 8 slender bristles, 2 or 3 of them much longer. There is also a considerable tuft of matted pile of no great length on the anterior, outer wall of the callosity. Scutellum large, bluntly subtriangular, distinctly thin, bearing pollen and pile similar to that of the mesonotum. The scutellar margin has about 5 pairs of long, slender bristles. Also, the mesonotum posteriorly in front of the scutellum bears a row of slender bristles. Squama short with a scanty fringe, which, however, seems to be banked in several rows. Pleuron pollinose with very dense, conspicuous, long, bristly pile over the whole of the mesopleuron, a large upward tuft turned upward and the remainder more or less erect but slightly curved backward or downward. Pteropleuron and hypopleuron without pile. The metanotum and the metapleuron in front of the haltere also without pile, but behind the spiracle there is a conspicuous tuft of somewhat appressed pile.

Legs: The legs are slender but with the femora distinctly stout. Anterior and middle femora slightly thickened toward the base, the hind femur throughout. All of the legs are pale yellow in the type-species, the last tarsal segment on the last four legs brownish. The femora are densely covered with flat-appressed, long, yellow, scaliform pile. The middle femur bears 2 black setae toward the apex, the hind femur bears 7 on the outer half on the anteroventral aspect; the last 4 are distinct bristles. Anterior tibia without spicules, except of the most microscopic type. Middle tibia, however, with 4 rows short, fine, oblique, sharp, slender bristles, 7 anterodorsally, 5 anteroventrally, 10 posterodorsally, and 7 posteroventrally. The quite long, slender, hind tibia also with 4 rows, 6 anteroventrally, 13 anterodorsally, 10 dorsomedially and these are the smallest, and 12 ventromedially. Claws small, slender, curved on the outer half, the pulvilli long and broad.

Wings: The wings are tinted with brown on the anterior half, the whole wing villose, the dark brown villi giving the posterior half of the wing a slight brownish tint also. The auxiliary vein ends near the base of the second submarginal cell and not very far from the end of the first vein. The second vein arises at a strong but not abrupt angle opposite the base of the discal cell. It has a distinct bend forward subapi-

cally so that the end of the marginal cell is widened and rounded posteriorly, the anterior branch of the third vein arises as an oblique, simulated crossvein with a backward spur. Outwardly it makes a very strong, deep bend turning forward to end before the apex of the wing. First posterior cell widely open, anal cell also widely open. The anterior crossvein enters the discal cell a little before the middle. The humeral crossvein is placed far out from the base of the wing. This basal section before the humeral crossvein is nearly a fifth of the length of the wing, hence the wing is strongly narrowed and lengthened at the base. The axillary lobe is narrow, especially basally, the anal vein curved, the alula short, the ambient vein complete and the costa with a strong lappetlike spur at the base, and the costa is also widened at the base and bears only minute setae.

Abdomen: The abdomen in the female type-species is elongate and a little tapered from the base to apex, the sides of the abdomen nearly or quite plane; the abdomen is a little longer than the thorax and of the same width at the base; it tends to be rather strongly flattened and covered very densely indeed with flat-appressed, matted, golden pile in the type-species, with a few, additional, fine, suberect, black or yellow bristly hairs in the posterior corners laterally. The sides are a little turned over and are yellow with long, golden pile, whereas the disc from above is entirely black, except for a yellow hind margin on the sixth and seventh tergites and a concealed eighth. The first segment has extraordinarily long, dense, erect, bristly pile extending almost to the midline but leaving the anterior margin widely bare as far as the base of the squama. Female terminalia small and concealed by bristles.

Dr. A. J. Hesse sums up the hypopygium of these flies in the following words:

Hypopygium of male usually subject to slight torsion, situated on side opposite last sternite, usually visible at end of abdomen; basal part divided dorsally into two separate parts by a suture or impressed suture, usually covered with fine hairs above, each basal part with a more or less well-marked-off apical part and the outer apical part or angle usually produce or angularly prominent; beaked apical joints usually elongate and curved, usually ending apically in a sharp point or upturned spine, sometimes with a row of spinules or spinule-like hairs along outer aspect nearer apical part; aedeagus with the apical part usually slender, often directed slightly upwards, the aedeagal part produced basally on dorsal aspect into a distinct, lobe-like or tongue-like process on each side which is joined on to lateral ramus on each side, the aedeagus also with a distinct ventral process, formed as a medial, apically directed structure by the fusion and coalescence of each lateral ramus, the apical part of this process assuming various and complex shapes; lateral and basal struts, the latter without a lateral shelf-like flange, but a short process on each side basally may be present.

Material available for study: I have a female of the type-species given to me by the British Museum (Natural History). I also have three other species sent to me through the generosity and kindness of Dr. A. J. Hesse of the South African Museum, Cape Town.

Immature stages: Unknown.

Ecology and behavior of adults; I have seen no record of the behavior of adults.

Distribution: Palaearctic: *Plesiocera algira* Macquart, 1840 [= *formicata* (Loew), 1857 (as *Anthrax*)]; = *inaequalis* (Becker), 1906 (as *Anthrax*); *araxana* Paramonov, 1925; *flavifrons* Becker, 1915; *pusilla* Bezzi, 1925; *tenella* (Loew), 1869 (as *Tomomyza*); *turkestanica* Paramonov, 1929.

Ethiopian: *Plesiocera curvistoma* Hesse, 1956; *flavilabris* Hesse, 1956; *pernotata* Hesse, 1956; *philerema* Hesse, 1956; *psammophila* Hesse, 1956; *rhodesiensis* Hesse, 1956; *rufiventris* Hesse, 1956.

Calledax, new subgenus

Type of subgenus: *Plesiocera psammophila* Hesse.

Small, slender, the abdomen somewhat constricted, blackish flies, more or less shining. The second vein origin is variable in position, but always clearly and abruptly at right angles and usually quite beyond the base of the discal cell. The posterior eye margin is recessed forward on the upper half of the head much as in *Tomomyza* Wiedemann, or *Amphicosmus* Coquillett, but is not indented or bisected. It includes the South African species placed in *Plesiocera* Macquart. In *philerema* Hesse the second vein arises at right angles opposite base of discal cell. In *curvistoma* Hesse it arises halfway between.

Flies of *Plesiocera* Macquart are Palaearctic and Ethiopian in distribution.

Plesiocera Macquart is related to *Stomylomomyia* Bigot and to *Erepacmus* Coquillett. Engel included *Stomylomomyia* Bigot as a subgenus of *Plesiocera*.

Length: 3.5 to 10 mm.; wing 3.5 to 9.5 mm. The type-species appears to be the largest species.

Genus *Conomyza* Hesse

Conomyza Hesse, Ann. South African Mus., part 2, vol. 35, p. 114, 1956. Type of genus: *Conomyza semirufella* Hesse, 1956, original designation.

Small flies that are related to *Plesiocera* Macquart. The occiput is shorter behind the ocellar tubercle and the occipital indentation or gap is greater, more distinct, and wider. The scales on the upper part of the body are distinctly finer and more hairlike. The front tibiae bear distinct, minute spicules and spurs; the tarsi, especially the female tarsi, are distinctly shorter than the tibia, and they bear distinct spinules below on the front tarsi. In this genus the front claws are almost as large as the middle claws, not nearly or quite vestigial as in *Plesiocera* Macquart. A weak genus, possibly only a subgenus.

This genus is known from the type-species and one well-marked variety from Namaqualand, the variety from Koup Karoo.

Length: 4 to 7 mm.; of wing 3.5 to 5 mm.

As I have not been able to see or obtain material of *Conomyza* Hesse, I quote the author's description of this genus. Hesse states:

This new genus is erected to contain a species which on account of certain distinct characters cannot be retained in the genus *Plesiocera* Macquart, as defined in this memoir. In quite a number of characters it is, however, almost indistinguishable from the latter genus. Its chief characters, when compared with the latter, are as follows:

Body similarly shaped. Vestiture also composed of hairs and adpressed scaling, the former also comparatively or moderately sparse; the finer and longer ones disposed in the same way and on the same parts of body, those on abdomen also fine, shortish and inconspicuous; scaling on body, however, distinctly finer, more hair-like or pile-like, the individual scales, even along sides of thorax above, on pleurae, abdomen and on legs finer and more hair-like, giving the insects a distinctly more pily appearance than in species of *Plesiocera* Macquart; scaling on sides of thorax, even if denser than on disc, not contrastingly cretaceous whitish or ochreous yellowish and that on pleurae also not contrastingly white.

The head is as in *Plesiocera* Macquart, broader across eyes than across thorax; occiput, however, distinctly shorter or narrower behind ocellar tubercle, the occipital lobes thus less prominent, the medial sulcation distinctly broader, more gap-like, the two lobes more broadly separated, the sulcus nearly as broad as width of ocellar tubercle; eyes with the hind margin as in *Plesiocera* Macquart, not indented or subangulately emarginate, only broadly sinuous, separated above on vertex in both sexes, narrower in males and about as broad as ocellar tubercle, appearing slightly narrower than in *Plesiocera* Macquart, there being no small space in females a little less than 2 times width of tubercle; facial part also produced, distinctly cone-like, the conical part, however, less sharply pointed, slightly blunter, more rounded; antennae as in *Plesiocera* Macquart, joint 3 gradually narrowed apically, more rapidly along lower part, no distinct slender apical part visible as in the case of some species of *Plesiocera* Macquart, ending apically in an almost indistinguishable terminal style, bearing a stylet; proboscis also short, confined to buccal cavity, its labella blunter apically. Wings as in *Plesiocera* Macquart; alula also much reduced and axillary lobe narrowish; middle cross vein at about or near middle of discoidal cell; second vein originating somewhat obliquely quite a distance away from base of third vein also kinked.

The legs have some spines on outer lower and apical aspect of hind femora and also with a row of distinct spines on inner lower aspect from base to beyond middle in males; tibiae always with distinct, though small, spicules and spurs on front ones; front tarsi scarcely as long as front tibiae, usually shorter, with distinct spicules like those on middle tarsi, though smaller; front claws not markedly reduced or vestigial as in *Plesiocera* Macquart; pulvilli well developed. Hypopygium of males rather large and conspicuous, with the opposing last sternite rather more elongate than in *Plesiocera* Macquart, its apical angles also angular; basal part divided dorsally into two by a suture, the apical part of each hairy and the base of each drawn out into a lobe-like process; beaked apical joints narrowish, curved inwards, more or less hollowed above, the edges more or less ridge-like, the inner one bearing an upwardly directed dentate process or spine near apex, the hinder part of each joint provided with hairs above (side and dorsal views in middle); aedeagus very elongate, slender, cylindrical and curved as shown in the side view, with a long ventral process (Ae. Pr.) arising near its base from middle part of aedeagal complex, the aedeagal part also produced basally and dorsally on each side into a lobe-like process (seen in outline in left-hand figures and also in right-hand one); ramus on each side from each basal part as shown in figures; lateral and basal struts well developed, shaped as shown in figures.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of males rather large and conspicuous, with the opposing last sternite rather more elongate than in *Plesiocera*, its apical angles also angular; basal part divided dorsally into two by a suture, the apical part of each hairy and the base of each drawn out into a lobe-like process; beaked apical joints narrowish, curved inwards, more or less hollowed above, the edges more or less ridge-like, the inner one bearing an upwardly directed dentate process or spine near apex, the hinder part of each joint provided with hairs above; aedeagus very elongate, slender, cylindrical and curved, with a long ventral process arising near its base from middle part of aedeagal complex, the aedeagal part also produced basally and dorsally on each side into a lobe-like process; ramus on each side from each basal part; lateral and basal struts well developed.

Material available for study: None seen. Known only from the unique types in the Cape Town Museum.

Immature stages: Unknown.

Ecology and behavior of adults: No information on record.

Distribution: Ethiopian: *Conomyza semirufella* Hesse, 1956, *semirufella karoana* Hesse, 1956.

Genus *Exepacmus* Coquillett

FIGURE 293

Exepacmus Coquillett, Trans. American Ent. Soc. Philadelphia, vol. 21, p. 101, 1894a. Type of genus: *Exepacmus johnsoni* Coquillett, 1894, by monotypy.

I have compared the type of *Exepacmus nasalis* Melander with the type-species of *Stomylomyia* Bigot and I find the only significant difference lies in the very deep excavation of the posterior occiput in the one species as against the very shallow indentation in the other species. For this reason I leave *Exepacmus* as a distinct genus, and I have included it in the key to the genera of the Lomatiinae, but I consider a detailed description unnecessary.

Distribution: Nearctic: *Exepacmus johnsoni* Coquillett, 1894 [= *nasalis* Melander, 1950].

Genus *Eucessia* Coquillett

FIGURES 124, 374, 635, 653

Eucessia Coquillett, Canadian Ent., vol. 18, p. 82, 1886a. Type of genus: *Eucessia rubens* Coquillett, 1886, by monotypy.

Small flies with hyaline wings and with rather short, slightly tapered, cylindrical abdomen as in some *Aphoebantus* Loew. The large globular head is a little wider than the thorax. The only known species has a blackish mesonotum with the abdomen predominantly light brownish orange and the legs of the same color. The genus differs from *Aphoebantus* Loew principally in the short, bulblike third antennal segment which is very little longer than wide. The dense, silver pollen on the slightly inflated front of the male is rather

similar to *Desmatoneura* Williston, but in *Eucessia* Coquillett the face is a little produced forward, slightly more so in the female, and it has a very weakly indicated furrow across the face beneath the antennae. Also from this genus it differs in the position of the anterior crossvein, which is at the middle of the discal cell in *Eucessia* Coquillett, and moreover the second vein originates obliquely before the end of the second basal cell as measured at the anterior angle. These little flies also have the scales on the mesonotum rather wide, dense, and conspicuous, especially laterally and again in patches along the sides of the tergites and in a dense, posterior border on the first antennal tergite.

This little genus is restricted to a single species hitherto known only from southern California. I have a single female of what appears to be a different species from Texas, taken 20 miles west of Toyah, August 4, 1954.

Length: 4.5 mm. to 6 mm.

Head, lateral aspect: The head is subglobular, the occiput relatively short above and below and the posterior eye margin has a deep but broad and rather shallow indentation a little below the middle of the head. There is only a minute anterior incision on the eye margin at this indentation. The pile of the occiput is dense, scaliform, and appressed and extends abundantly to the eye margin. The inner fringe of the occipital recess is short, fine, and sparse. The front is short, very slightly protuberant dorsally, densely covered with silvery white, pollenlike micropubesence in the male and also the female. Both sexes have an isolated, longitudinal band of stiff, bristly, oblique pile beginning near the posterior part of the front, well separated from the corresponding band on each side and also separated from the eye margin. The face is slightly projecting, but not all conspicuously. It is a little more projecting in the female from Texas, and it is fringed and bordered along the oragenal recess with coarse, pale, bristly pile. There is only the faintest indication of a transverse, circular furrow beneath the antennae.

The eye is quite large, occupying most of the head, the upper facets only a little enlarged. The proboscis is short, robust, the labellum comprising more than half the length of the proboscis with fleshy lobes at the apex that bear a few stout bristles ventrally. The palpus is long and slender and composed of 2 segments, the first segment curved and arched outward, the second segment shorter, also slender and only about one-third as long as the first segment. The antennae are small, they are attached a little above the middle of the head, the first segment, though quite short, is twice as long as the second segment. The third segment viewed laterally is wide and only a little longer than this basal, vertical width and the styliform extension is short and blunt. It bears a distinct microsegment with bristle at the tip. In the Texas female, viewed laterally, the third segment is equally narrowed above and below so that the whole segment is entirely conical. In both of these

individuals the segment is more narrow when viewed from above and it is 2 to 3 times as long as wide from this view. The pile of the antennae is minute and scanty.

Head, anterior aspect: The head is circular, distinctly wider than the thorax, the eyes are separated in the male by an extent equal to the basal width of the third antennal segment viewed from above. In the Texas female it is rather more than twice as wide. The ocellar tubercle is somewhat swollen with vertical sides and the ocelli occupy an equilateral triangle, and there is a clump of stiff, reddish bristles in the middle of the tubercle, curved forward and not longer than the tubercle itself. The sides of the eye rise above the vertex. The antennae are separated by a distance equal to about half the width of the first segment. The antennae are only slightly divergent. The oragenal recess is comparatively small, elongate oval, rather shallow anteriorly, deeper below and almost equally wide at both ends. The genae are present but quite linear, and there is no tentorial fissure. Viewed from behind the occipital recess is deep but rather small. Viewed from above the occipital lobes are narrowly separated.

Thorax: The mesonotum is shining blackish, the scutellum likewise and without pollen, but in the Texas female the mesonotum has a thin, light pollen over the black part, the ground color changing to light brownish orange laterally as indeed over the entire remaining part of the female, except for the lower pleuron, which has some blackish brown diffusely present, and the scutellum of the female is almost entirely orange brown. The pile of the mesonotum, scutellum, and pleuron consists of matted, dense, broad, conspicuous scales from among which arise a very few, fine, scattered, curved, bristly hairs of no great length. However, the notopleuron has a tuft of 3 rather long, stout, red bristles and 4 or 5 other more slender ones. Postalar callosity with 2 or 3 long, red bristles, margin of scutellum with 3 or 4 pairs. The pollinose humerus in the male of the type-species bears scaliform pile and also stiff bristly pile. In the female scales are lacking on the humerus, except perhaps the posterior border but some bristly pile is present. Moreover, along the anterior margin of the pronotum of both sexes there is a collarlike fringe of pile. Disc of scutellum with scales and an odd patch on each side at the immediate base. Upper mesopleuron with appressed scales and rather dense, erect, bristly pile. Lower mesopleuron and upper sternopleuron with a patch of appressed scales. Pteropleuron, metanotum, metapleuron, and hypopleuron bare, pollinose only, except that there is a small tuft of erect, scalelike pile posterior to the spiracle. The squama is quite short on the thoracic part, larger on the alar portion, the short fringe scanty.

Legs: The legs are small but the femora distinctly a little thickened, especially the second and third pairs. They bear scattered, appressed scales. The anterior tibia has a few microsetae dorsally and posteriorly, which stand out from the rather dense cover of smaller,

flat-appressed setae. Middle tibia with 5 or 6 short, oblique, pale, spinous bristles posteriorly and a few dorsally. On the hind tibia the spinous bristles are a little longer, pale in color, 5 or 6 in each row including those at the apex and there are 3 rows present. The pulvilli are vestigial, claws sharp and a little curved.

Wings: The wings are hyaline, glassy, there are 2 submarginal cells and all the posterior cells are open. The anterior crossvein lies at the middle of the discal cell, the second vein arises in a straight line with the radial sector, the third vein arises obliquely, both of these veins arise before the end of the second basal cell as measured at the anterior basal angle. The anterior branch of the third vein arises steeply but makes a rounded bend outward. The marginal cell is wide on the apical half and has a mere suggestion of a bend below, opposite the furcation of the third vein. Anal cell widely open, axillary lobe wide and alula wide and the ambient vein complete. Base of the costa with strong, sharp, scalelike spurs.

Abdomen: The abdomen is only a little longer than the thorax, cylindrical, sometimes slightly compressed laterally but in the Texas female rather flattened, and less narrowed apically. In the type-species there is a band of broad, flattened, appressed scales across the middle of each tergite but not extending quite to the lateral margin. In addition there are a few scattered, subappressed, stiff, pale, reddish hairs becoming more numerous on the last tergite. First tergite with a fringe of rather long, erect, coarse pile basally and a narrow band of appressed scales basally. The male terminalia are large and conspicuous, inverted and form a somewhat narrowed, conical, truncate protuberance. Female terminalia surrounded by a dense fringe of inwardly turned, bristly hairs.

Material available for study: The type-species male, and the female of a second species from Texas.

Immature stages: Unknown.

Ecology and behavior of adults: Taken by Timberlake on flowers of *Euphorbia albomarginata* at Riverside, California, in May (Melander, 1950).

Distribution: Nearctic: *Eucessia rubens* Coquillett, 1886.

Genus *Xeramoeba* Hesse

FIGURES 128, 655

Xeramoeba Hesse, Ann. South African Mus., part II, vol. 35, p. 356, 1956. Type of genus: *Xeramoeba apricaria* Hesse, 1956, by original designation.

Small flies of dark color and very thin, grayish pollen. The pile is short, scanty, largely appressed and such few bristles as are present are thin, short, and scanty. They are very much like *Aphoebantus* Loew in general appearance with subglobular head, wider than the mesonotum, and similarly the eyes are indented and bisected and the antennae are very similar; in both the face is rounded and retreating in lateral

aspect. However, the oragenal cavity is much narrowed when viewed from below and the proboscis very short, stumplike, the labellum is large and muscoidlike. Like *Chionamoeba* Sack, the metanotum is quite short and there is no pile on metapleuron, metanotum, or hypopleuron and in *Xeramoeba* Hesse, none on the pteropleuron. In both the plumula is present but there is no strigula. Unlike *Chionamoeba* Sack the front above antenna is not swollen. As in many of the Lomatiinae the second vein arises abruptly not too far distant from the anterior crossvein. Bowden (1964) believes that these two genera belong in the Anthracini; while granting that to some extent they may be annectant, they may just as well be convergent and it seems to be better to create for them a separate tribe within the Lomatiinae, the more so, since there are nine other genera within the Lomatiinae with a second vein which shows abrupt origin. Bowden (1964) takes note of the microspicules upon the front tibiae. While they certainly serve to differentiate this genus from *Prothaplocnemis* Bezzi, inasmuch as most bombylids showing a varying development of spines upon the legs, this appears to be one of the most uncertain characters upon which to base phyletic relationships.

Hesse (1956) compares these flies to *Villa* Lioy or *Thyridanthrax* Osten Sacken as far as superficial aspect is concerned. He notes that *Xeramoeba*, in comparison with *Chionamoeba* Sack, is less elongate, the pile and bristly hair slightly longer, those on front and face denser, longer (and stiffer), the eyes of the male more widely separated. I can see little difference in the upper occipital lobes of the two genera. Hesse finds the basal wing comb better developed, the costal cell shorter, the tibial spicules better developed and conspicuous than in *Chionamoeba* Sack; he finds the hypopygium differs from that genus and also from *Anthrax* Scopoli. He finds that the tubelike aedeagal process suggests *Chionamoeba* and the downwardly directed apical hook of the aedeagus resembles that present in some *Anthrax* species.

These small flies are known only from South Africa.

Length: 4.3 to 7.5 mm.; wing 4.5 to 8.5 mm.

Head, lateral aspect: The head is large and nearly globular; the occiput is comparatively long dorsally and considerably reduced in length below. The surface is thinly pollinose, the pile is short and rather scanty, except on the rather isolated, central fringe where the pile is dense. The indentation of the eye is deep, without a bare triangle but with the lines separating upper and lower divisions of the eye quite long and slender. Eye greatly extended forward so that the whole head is very broadly rounded in front both above and below the antennae. Both front and face extend only a very short distance outward; the cheeks are not visible below the eye margin, and the middle base of the head behind the proboscis barely shows. The front is rounded and bears short, oblique, stiff, rather abundant pile; that of the face similar in length and character. The antennae are attached at the middle of the head; they are quite

small, the first and second segments equal in length, the first segment only slightly wider, and both segments more than twice as wide as long. Third segment strongly bulblike at the base, abruptly swollen below to a short, thick style, which bears a very short microsegment. The proboscis is extremely short and exceptionally stout and robust. The large, flat lobes of the labellum are muscoid in character and flared outward. Palpus small and minute.

Head, anterior aspect: The head is slightly wider than the thorax. Eyes in the female widely separated by 3 times the width of the knoblike, prominent, ocellar tubercle the sides of which are vertical, and bear 2 or 3 short hairs directed forward. Eyes in male also widely separated but less than in females. The antennae are separated by a little more than half the width of the first segment. The face is extensive and slightly retreating below, nearly vertical above, the antennal sclerite distinct. There is only a faint diagonal or crescentic line extending from the antenna obliquely down to the eye margin. The eyes are green in reflection, the oragenal recess is small and strongly oblique, narrow, deep in front and behind with an odd, deeper, medial fossae. The oragenal recess is so narrow that posteriorly it touches the sides of the proboscis, hence the face and recess are strongly convergent. The tentorial fissure is linear and slitlike, the space between it and the eye quite linear and this bare, linear stripe continued on upward to opposite the antennae. There is a rather strong overgrowth of the eye ventrally along the margin of the oragenal recess and again on the upper sides of front and vertex and upper occiput. Viewed from above the lobes of the occiput are narrowly separated; the fissure is deep and rounded on each side with a deep, triangular pocket behind the vertex.

Thorax: The thorax is black and compact and triangular below the mesonotum. The mesonotum is low, a little more strongly convex anteriorly. It is faintly pollinose, the pile consisting of scattered, curled, appressed, rather short and slightly flattened hairs including all of the anterior and lateral pile, except the anterior collar and except the humeral pile. Notopleuron with 1 or 2 fine, long bristles. Postalar callosity with 2 or 3, and the scutellar margin with about 4 pairs of more slender, long, bristly hairs and others in front of the scutellum. Pile and pollen of the scutellum similar to that of the mesonotum. Plumula present, the tuft of hairs moderately long but not numerous. Pleuron pollinose, upper mesopleuron with a conspicuous tuft of scattered, sparse, upturned, slender, bristly hairs. Posterior half of mesopleuron with some flat-appressed, scaliform pile below and a loose clump of bristly hairs curled backward above. There is a large, dorsal triangle on the sternopleuron densely covered with flat-appressed scales. Metanotum, pteropleuron, hypopleuron, and the anterior metapleuron pollinose only. There is a small tuft of scales behind the spiracle. Halteres small and short.

Legs: The legs are slender and rather short. Anterior femur are at most very slightly thickened toward the base; all the femora have flat-appressed, pale scales. The anterior femur has 2 or 3 small, fine setae anteriorly; the middle femur likewise. The posterior fringes of pile are lacking on the first four femora. The hind femur bears 1 or 2 comparatively strong, attenuate, sharp bristles ventrolaterally near the apex, 3 smaller ones dorsally above. All the tibiae are slender; anterior tibia has 7 tiny, fine setae dorsally, 2 ventrally and 4 or 5 posteriorly. The middle tibia bears scarcely stronger setae; there are 4 antero-ventrally, 6 anterodorsally, 6 posterodorsally and 3 or 4 posteroventrally. On the hind tibia the setae are a little longer, a little stouter but still slender; there are 5 ventrolateral, 6 or 7 dorsolateral, and 4 very minute, slender ones ventromedially. Claws quite slender, a little curved at the apex, the pulvilli wide and rounded at the apex and only about half as long as the claws.

Wings: The wings are hyaline, the surface wrinkled and iridescent. There are only 2 submarginal cells. The second vein shows only a very slight, scarcely noticeable kink or bend opposite the base of the second submarginal cell. The anterior branch of the third vein arises plane but not quite at a right angle; generally without a stump or trace of stump. The second vein likewise arises plane, not at a right angle, its origin is near the anterior crossvein but basal to it and separated from it by the length of the anterior or less. The anterior crossvein enters the discal near the basal fourth, the first posterior cell is quite widely open, almost maximally; the anal cell is open; the ambient vein is complete, and the alula is well developed. The costa is expanded at the base but bears only weak setae. The wing is large and long, at rest extending far beyond the apex of the abdomen. Costal hook large and scalelike. Prehumeral part of costa as long as the last section of the third vein.

Abdomen: the abdomen is black, as long as the thorax, slightly wider than the mesonotum to the end of the second tergite. Second tergite more than twice as long as the third; 7 tergites are visible dorsally. The abdomen as a whole is quite broad and broadly oval apically with the apex of the abdomen rather triangular; the last tergite in the female conical. The whole abdomen is gently convex, thinly pollinose; the pile consists of flat-appressed, rather loose and scattered, slender, slightly flattened hairs. Sides of the tergites with some longer, erect, bristly hairs. Sides of the first tergite with a dense brush or band of dense, erect, coarse pile becoming much shorter medially.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of male with a rather conspicuous basal process to the shell-like basal parts which also have some hairs dorso-apically; beaked apical joints compressed and twisted; aedeagal apparatus in form of a tube-like or funnel-like process lodging the aedeagus proper and ending apically below in a downwardly directed recurved hook or process. Hypopygium of this genus is

different from that of the preceding genus *Chionamoeba* and the following genus *Anthrax*. The tube-like aedeagal process, however, is reminiscent of that of the former and the downwardly directed apical hook of this structure also resembles that present in some species of *Anthrax*.

Material available for study: Representatives of the genus presented to me through the courtesy of John Bowden.

Immature stages: Unknown.

Ecology and behavior of adults: Bowden (1964) notes that *Xeramoeba gracilis* Bowden was taken settling upon bare ground in company with species of *Petrorossia* Bezzi.

Distribution: Ethiopian: *Xeramoeba apricaria* Hesse, 1956; *gracilis* Bowden, 1964.

Genus *Chionamoeba* Sack

FIGURES 228, 387, 645, 651

Chionamoeba Sack, Abhandl. Senckenberg. Naturf. Ges., vol. 30, pt. 4, p. 543, 1909. Type of genus: *Bibio nireca* Rossi, 1790, by original designation.

Engel (1934), p. 415, key to 5 Palaearctic species.

Small flies with broad and only slightly convex abdomen; in South African species, however, the abdomen is more elongate, but on the basal half fully as wide as the mesonotum and distinctly and gently tapered. The face is very much rounded throughout and retreating below, scarcely protruded beyond the eye margin. The second vein arises either at the anterior crossvein, or a short distance before. Pile everywhere dense, fine, silky, matted, and appressed, except that on the mesopleuron there are 2 large bands or clumps of coarse, long, bristly, pale hairs, one directed upward, the other backward, and both subappressed; also the postmargins of the abdominal tergites have a row of short slender bristles and there are 3 more distinct bristles on the notopleuron with others on postalar callosity and on the margin of the scutellum.

These flies are found in southern Europe and 2 species are described from South Africa which are somewhat different.

Bezzi (1924) and Hesse (1956) note that in certain respects this genus appears to be more or less annectant with the Anthracini; this is perhaps more nearly true of the present genus and of *Xeramoeba* Hesse, both of which have a more or less muscoidlike labellum; Bezzi considered *Chiasmella* Bezzi to show such a relationship. Bowden (1964) notes that the aedeagus of his South African species *Chionamoeba choreutes* Bowden has the aedeagal sheath more extensive, in this respect being more like Anthracini. The front above the antenna is bossed much as in *Desmatoneura* Williston.

However, my studies lead me to believe that in spite of several anthracine characteristics the greater relationship is with the Lomatiinae and for them I erect a separate tribe, the Xeramoebini, separated from other groups by the presence of the plumula and the reduced

size of the hypopygium; see further discussion under the subfamily Lomatiinae.

Hesse (1956) notes that *Chionamoeba* Sack differs from *Anthrax Scopoli* in the following ways: it has a more elongate abdomen, either no bristles, or fewer, on the body, less dense, erect pile, a not concavely, saucer-shaped second antennal segment, a terminal micro-segment attached to segment three which bears no apical circlet of hair (such a circlet may indeed be a parallel development), a second vein not originating at right angles nearer opposite the anterior crossvein, and the base without an appendix, fewer spines on the femora, shorter and less conspicuous spicules on the tibia. From *Petrorossia* Becker it differs in the broader wings, longer costal cell, presence of a plumula, etc.

Length: 4.5 to 9.5 mm.

Head, lateral aspect: The head is nearly globular with the eyes considerably lengthened, quite circular in front, the entire front, especially the lower part, strongly produced forward and swollen conspicuously, gradually and regularly across from each eye margin. The face is somewhat less produced, but retreats slightly immediately below the antennae, then it is slightly raised or produced slightly above the oragenal margin. Pile of front and vertex abundant, but not dense and of no great length. On the front the pile is shorter and curled downward and is subappressed but erect near the vertex. The occiput is only moderately extensive dorsally. The indentation of the posterior eye margin near the middle is deep but much less so than in *Petrorossia* Bezzi. There is a nonpollinose triangle near the bottom of the indentation and the line of separation of the eye facets quite short. Upper eye facets moderately enlarged. Green reflections from the eye are only faint.

The proboscis is very short, not extending to the apex of the oragenal recess, the labellum large, somewhat flattened, nearly as long as the basal part of the proboscis. Palpus very small, slender, with a few long, fine hairs. Antennae attached a little below the middle of the head in profile, quite small, the first segment very short, especially dorsally, scarcely visible and apparently overlapped by the extra development of the lower front. It is somewhat longer below since the swollen front gives way between the antennae. The first segment bears some long, numerous, bristly hairs ventrally and laterally. The second segment is rather large, apically widened and rounded, short pyriform in shape with the small end embedded in the first segment. The whole segment is as long as the conical, bulblike part of the third segment. The second segment bears conspicuous, long, scattered, bristly hairs dorsolaterally, and ventrally and laterally, none medially. The third segment is bulblike at the base with thick, rather short, micropubescent style.

Head, anterior aspect: The head is wider than the thorax, nearly circular with all 4 sides slightly flattened in their middles. The front is very extensive; in the male the eyes are separated by about twice the width of the high, knoblike, ocellar tubercle, which has ver-

tical sides, and forms an equilateral triangle and has a few fine, erect hairs. The front is very strongly widened to the middle of the head and the face and oragenal recess almost equally strong and narrowed below and at the bottom of the head scarcely wider than the vertex. There is a faint, impressed, fossallike division extending circularly outward on each side below the antennae. Antennal sclerites prominent and differently colored. The oragenal recess is narrow, quite deep posteriorly, rather deep anteriorly but a little widened and a fringe of fine, facial hairs lies around its edge. The tentorial fissure is linear leaving only a narrow stripe next to the eyes. Gena very much reduced, almost absent, except for the flattened, triangular base on each side behind the oral recess. Antennae quite widely separated. Viewed from above the occipital lobes almost touch. The triangular pocket behind the vertex is deep.

Thorax: The thorax is black and compact, the lower part triangular, the mesonotum low, and flattened posteriorly. The extreme lateral margin, humerus, and postalar callosity are reddish brown, the whole surface of these parts pollinose. The pile is rather dense, fine, long, and erect over the whole surface, but it is coarser and more bristly on the anterior collar and perhaps even longer. There appears to be a deep fossallike recess medial to the thin, high, vertically ridgelike postalar callosity. Opposite it the vertically raised mesonotum bears shaggy tufts of pile. The notopleuron has 1 or 2 bristles, the postalar ridge has a tuft of pile and 1 or 2 bristles. The alary squamae are quite short, the fringe long but consisting of only 1 or 2 ranks of hairs. Thoracic squama very conspicuous with no hairs. Plumula with only a few hairs. Scutellum black and covered like the mesonotum. Pleuron pollinose, the upper mesopleuron with dense, long, bristly, upturned pile on the upper half and with more scattered, long, slender, bristly hairs below and posteriorly. Anterior pteropleuron with 2 tufts of hairs. Sternopleuron on the upper half with scattered, stiff, subappressed hairs. Metanotum and the whole of the metapleuron and hypopleuron pollinose only.

Legs: The legs are slender including the femora. All the femora have rather numerous, flat appressed, conspicuous scales. Middle femur with conspicuous fringe of rather long hairs posteroventrally. None of the femora bear bristles. The anterior tibia bears minute, fine, suberect, slender spicules; there are 3 or 4 dorsally, 4 or 5 posteroventrally. On the middle tibia the spicules are slightly stouter and longer; there are 5 anteroventral, 6 or 7 posterodorsal, and 6 to 8 equally developed posteroventral ones. Bristly spicules of hind tibia equally slender, scarcely longer; there are 2 anteroventral, 6 to 8 anterodorsal, and 4 or 5 ventromedial ones. Front tarsi quite short, hind tarsi quite long. Claws slender, curved a little at the apex, the pulvilli long and spatulate.

Wings: The wings are quite large, long, and rather broad basally and at rest extending far beyond the abdomen. The surface of the wing is wrinkled and

iridescent. There are 2 submarginal cells. The marginal cell is scarcely widened apically and there is no kink or bend in the second vein. The anterior branch of the third vein arises rather gently and is rounded at the first bend. The second vein arises plane, abruptly but not rectangularly, near and basal to the anterior crossvein, removed from it by a distance nearly equal or equal to the length of the anterior crossvein, the first bend of this vein is slightly rounded. The anterior crossvein enters the discal cell near the basal fourth; the first posterior cell is widely open, the anal cell likewise. The ambient vein complete, the alula moderately well developed. Costa expanded at the base but with only a few minute setae. Costal hook scalelike.

Abdomen: The abdomen is elongate, a little longer than the thorax with the scutellum included, at the base not wider than the thorax and distinctly tapered or narrowed posteriorly, rather strongly convex dorsally, more flattened below. The abdomen is black, shining, with a very faint pollen and with dense pile of two types. Tergites beyond the middle of the second densely covered with matted, flat-appressed scales, with a conspicuous, lateral fringe of long, erect, pale, bristly pile on the sides of the abdomen, becoming even longer and denser, and coarser on the sides of the first tergite. Lateral pile of first tergite not extending in the middle of this segment. Apex of last tergite with a fringe of long hairs. Second tergite not twice as long as the third. Third and fourth tergites equal in length. Seven tergites and a very short eighth are visible in the male. The male terminalia often twisted to the left side, the basimeres broad basally, attenuate apically, but lying adjacent so that each is somewhat triangular.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of male of South African species without any process to basal parts on outer side, but with the inner apical part produced; beaked apical joints elongate, cylindrical and curved; aedeagal structure in form of a funnel lodging the aedeagus; lateral struts small. Terminal lamellae at posterior end in last sternite with their dorso-apical angles not produced.

Material available for study: The representatives of this genus in the collections of the British Museum (Natural History). Also, material sent through the courtesy of John Bowden in exchange.

Immature stages: Unknown.

Ecology and behavior of adults: Bowden (1964) notes that while males were seen hovering over a sand heap, the females were found investigating small holes in the timber of buildings.

Distribution: Palaearctic: *Chionamoeba erythrostoma* (Rondani), 1873 (as *Anthrax*); *frontalis* (Wiedemann), 1828 (as *Mulio*) [= *Cytherea frontalis* Wiedemann, 1828, in Engel]; *lepida* (Hermann), 1907 (as *Argyroamoeba*); *nivea* (Rossi), 1790 (as *Bibio*), *nivea lioyi* Griffin, 1896; *sabulonis* (Becker), 1906 (as *Argyroamoeba*), *sabulonis rubicunda* Bezzi, 1925; *semirufa* Sack, 1909.

Ethiopian: *Chionamoeba choreutes* Bowden, 1964; *meridionalis* Hesse, 1956.

Genus *Petrorossia* Bezzi

FIGURES 134, 234, 383, 634, 652, 918, 919, 920

Petrorossia Bezzi, Zeitschr. syst. Hymen. Dipt. Teschendorf, vol. 8, p. 35, 1908c. Type of genus: *Bibio hesperus* Rossi, 1790, by original designation.

Pipunculopsis Bezzi, Bull. Soc. Roy. Ent. d'Egypte, vol. 8, p. 211, 1925c. Type of subgenus: *Pipunculopsis bivitata* Bezzi, 1925, by monotypy.

Bezzi (1924), pp. 151-152, key to 6 Ethiopian species.

Bezzi (1925), pp. 209-211, key to 8 species.

Engel (1934), p. 409, key to 5 Palaearctic species.

Hesse (1956), pp. 312-315, key to 9 Ethiopian species.

Bowden (1964), pp. 60-61, key to 9 Ethiopian species.

Small, dark colored flies with faint grayish-white pollen; the abdomen in some species may be reddish laterally, or terminally. In one species the first two antennal segments are white, the third black. The pile is scanty, rather short, flat-appressed, more erect laterally and as in *Chionamoeba* Sack it is apt to be slenderly scabrous on the abdomen. The face is rounded and retreating, but varies a little in prominence; the proboscis and labellum, short and contained within the oral recess. The wings are hyaline or tinged with brown anterobasally. The second vein arises abruptly between the base of the discal cell and the anterior crossvein. Anal cell widely open. End of marginal cell with thumblike enlargement, but this may be wanting in one or two species. The legs are pale; the black front tibial spinules present but minute. The plumula is absent. The occipital lobes are in contact but the crease is deep, the sides rounded. In general appearance these flies are apt to suggest a small species of *Villa* Loew. There is more than a passing resemblance among not only *Petrorossia* Bezzi, but its relatives *Xeramoeba* Hesse and *Chionamoeba* Sack to a few uncommon species of *Anthrax* Scopoli, which are more elongate and slender than usual. While some species of *Petrorossia* Bezzi have an apical microsegment attached to the end of the third antennal segment, it is surmounted by a thick spine and there may be a circle of a few fine hairs, as in *fulvipes* Loew. It is related to *Prothaplocnemis* Bezzi, which also has a terminal tuft of hairs on the antenna. Engel makes *Pipunculopsis* Bezzi a subgenus.

This genus is represented by several species in the South Palaearctic region and by more numerous species in South Africa. It also occurs in Australia.

Length: 4.8 to 10.5 mm., of wing 4.6 to 12 mm.

Head, lateral aspect: The head is nearly globular, the occiput quite short immediately behind the vertex but lengthening almost immediately and quite long, and deep at the midpoint of the eye laterally. The incision of the eye at this point is extremely broad and deep; both dorsally and behind the vertex the occiput slopes steeply inward toward the comparatively small,

cuplike recess. The whole surface of the occiput is covered with dense, pollenlike, micropubescence, and dense, erect pile becoming longer at the central internal fringe. Pile and pollen reach to the eye margin, except at the bottom of the indentation there is a bare triangle and the horizontal line separating upper and lower facets at this point is unusually long. The eye is reniform, the upper facets only a little enlarged; the entire eye has a greenish reflection. The front at the point of attachment of the antennae is very short, nevertheless, because the antennae are attached at or slightly below the middle of the head, its length from antennae to vertex is great, and since the length of the head is considerable, the front is strongly rounded in profile.

The face extends only a short distance beyond the eye margin; it is rounded and strongly recessive, the oragenal cup reaching only two-thirds of the distance from its posterior margin to the base of the antennae. Proboscis is very short, not extending beyond the oragenal recess. The entire proboscis, including the labellum, is quite stout and robust; the latter is somewhat flattened and leaflike and nearly or quite as long as the basal part of the proboscis. Palpus short, robust, almost barrel-shaped with some fine hairs at the apex and laterally. Antennae placed at or just below the middle of the head, small, the first segment only a little larger than the second and slightly longer. The first segment bears short, stiff hairs medially, a conspicuous tuft of longer hairs dorsally and ventrally, which are confined to the middle of the segment. Second segment a little more than half as long as high but longer in the middle on the medial aspect than either above or below; it bears a few long setate hairs dorsally and ventrally and laterally but none medially. Third segment with a strong, bulblike base nearly as wide as the second segment and abruptly narrowed into a thick, stout style about twice as long as the swollen basal part. The style bears a short, stout microsegment with a thick, apical spine and 2 or 3 short apical hairs, which are minute and not all conspicuous.

Head, anterior aspect: Head a little wider than the thorax, nearly circular but slightly flattened on all 4 sides. There are no grooves or fossae separating the face or curving from side to side beneath the antennae, although the antennal sclerite is distinct. The eyes in the male are separated by a distance fully equal to the high, knoblike, ocellar tubercle, the sides of which even curve under a little. The posterior eye corners are quite broadly rounded and curve outward and away from the tubercle, which is short isosceles; the ocelli lie on the edge of the tubercle and bear a few moderately long, stiff hairs centrally. The eye margin is raised above the level of the upper front and vertex, the whole surface finely pollinose and the lower two-thirds of the front bears dense, slightly flattened, curved, subappressed, shining hairs over the whole surface, except for a linear, medial, nonpilose stripe and a linear, nonpilose, marginal stripe continued on down to the gena below. The antennae are separated by nearly the

basal width of one segment and the antennae are strongly divergent. Face extensive dorsoventrally, pollinose and uniformly covered with similar pile of the same color, length and appression as the pile of the front. The oragenal recess is comparatively small and narrow, slightly pinched in the middle, deep anteriorly and posteriorly, its total width a little less than one-fifth the total head width. The tentorial fissure is linear and deep and begins at the point where the oragenal recess narrows anteriorly. Walls of oragenal cup quite thin and vertical. Genae decidedly linear, the eyes extended below the genae in profile. Viewed from above the occipital lobes are distinctly separated with a narrow fissure between and with a deep, triangular pocket behind the posterior vertical wall of the ocellar tubercle.

Thorax: The thorax is compact, almost triangular below the mesonotum. The mesonotum is low, very little convex, widened only behind the wings where the postalar callosity is rather prominent and is raised with a triangular troughlike depression dorsally. The thorax is black, thinly pollinose, the pile of the mesonotum consists of glittering, flat-appressed, narrow, scaliform pile with rather dense, fine, long, erect pile, longer on the anterior third and merging directly into the anterior collar. This pile is equally abundant on the swollen humerus, the posterior corner of which is vertical; equally abundant over the whole notopleuron and the sides of the mesonotum, but, however, shorter in the middle of the mesonotum between the wings. There is one long bristle on the notopleuron, usually 2 or 3 on the postalar callosity, sometimes a row of fine hairs in front of the scutellum and the flattened, subtriangular scutellum covered with the same pollen and pile as the mesonotum and its margin at most with a few long, slender, bristly hairs in addition to appressed pile. Squama short, plumula absent. Pleuron pollinose, the mesopleuron is almost wholly covered by dense, quite long, bristly pile, these elements on the upper border are stouter, all of those which lie on the upper half are curled upward and the remainder are strongly curled backward and downward. Upper half of sternopleuron and sometimes the whole of it covered with appressed, shorter pile directed backward. Pteropleuron, metanotum, anterior metapleuron, and the hypopleuron pollinose only. There is a tuft of pile behind the spiracle.

Legs: The legs are slender, the anterior femur, however, distinctly a little widened basally beginning at the outer third. All of the femora and the hind tibia are covered with flat appressed, narrow scales. These scales are quite dense in some species, in others sparse. The anterior and middle femora have a row of short hairs posteroventrally. Hind femur with 1 or 2 fine, weak bristles ventrolaterally near the apex and sometimes 2 or 3 shorter ones dorsolaterally on the outer half. All of the tibiae quite slender; anterior tibia with 1 or 2 minute, fine setae posterodorsally and 4 or 5 others posteroventrally. Middle tibia also with a few

slender, short, oblique bristles. Hind tibia with 8 fine, oblique, slender, black bristles dorsolaterally and 7 ventrolaterally, besides 3 or 4 ventromedial bristles. Claws quite slender, sharp, strongly curved near the apex, the pulvilli long and spatulate.

Wings: The wings are hyaline, large, and at rest extend far beyond the abdomen. The wing surface is wrinkled and iridescent. The second vein arises between the anterior crossvein and the base of the discal cell and almost halfway. It arises abruptly but not rectangularly. There are only 2 submarginal cells, the second vein with a strong, preapical bend so that the marginal cell is bent backward and is thumblike in outline. The anterior branch of the third vein arises obliquely, but not quite rectangularly, and there is a strong backward bend in this vein corresponding to the bend of the second vein. The anterior crossvein enters the discal cell at or before the basal third. The first posterior cell is a little narrowed apically and the anal vein is open. Ambient vein complete, the alula short but distinct. Costal comb weak, but costa strongly expanded. The costal hook or scale is well developed.

Abdomen: The abdomen is a little wider than the thorax at the base, obtuse apically, often rather high and thick or subcylindrical, the sides tapered or narrowed, the whole abdomen a little longer than the thorax with scutellum included. Tergites covered with dense, flat-appressed, slightly flattened pile and sometimes with additional sparse, very fine, bristly pile, likewise more or less appressed. Sides of the tergites sometimes with longer, pale bristly hairs which are more or less erect. Ground color often reddish or orange brown laterally, the tergites widely blackish in the middle, the apical tergites may be wholly red. Hypopygium large with the basimeres triangular and turned to one side or dorsal in position.

Since Dr. A. J. Hesse was able to base his conclusions upon a greater number of species, I quote his remarks upon the male hypopygium:

Hypopygium of males with the basal parts convex, shell-like, covered dorsally and along outer apical margin with fairly stoutish, conspicuous and longish, bristly hairs, the base usually drawn out into a sort of scoop-like process; beaked apical joints either more or less twisted, curved or scroll-like, the dorsal or outer apical part excavated or hollowed, produced apically into a spine-like process or into upper and lower processes or even three processes, the upper one usually directed outwards over lower one, the dorsum of these joints usually with hairs or a tuft; aedeagus with a ventral process below, formed by the union of a ramus on each side from sides of basal parts, the apical part of this process either pick-like, blade-like, or ending in a bidentate or bifid process which is directed downwards; lateral struts shoe-horn-shaped, sometimes broadish and long; basal strut ham-shaped, sub-racket-shaped, or chopper-shaped, its apical margin sometimes with a ledge-like extension.

The male terminalia from dorsal aspect, epandrium removed, show a short, broad, robust figure, narrowed apically. The dististyli are blunt or indented apically. In the lateral view there are curious, basally expanded structures arising at or near the ramus or the upper wall of the basistyle, which curve forward as strongly

convergent, lobelike or clasperlike structures, overlying the apex of the epiphallus. They appear to have no relationship to the epiphallus or ejaculatory process.

Material available for study: Material in the collections of the British Museum (Natural History), and other examples sent through the kindness of John Bowden.

Immature stages: Unknown, although Bowden (1964) suggests that the probable hosts are small halictids, nomadids, or even megachilids, or crabronids.

Ecology and behavior of adults: Bowden (1964) comments on the habits of certain species. Females of *Petrorossia letho* Wiedemann are taken hovering over hot, bare soil or settling on it near the nest holes of small halictid and nomadid bees. *Petrorossia consobrina* Bowden was found hovering about the entrance holes of bee nests presumably megachilids and crabronids in the timbers of buildings. *Petrorossia phthinoxantha* Bowden was taken hovering at cracks and crevices in a bank frequented by various species of small bees; one female was taken at the flowers of *Tagetes* sp.; another species was found hovering over a path in rather dense forest; another about the bank of small stream; still others about the base of an uprooted tree.

Distribution: Palaearctic: *Petrorossia albifacies* (Macquart), 1840 (as *Bombylius*) [= *rufipes* Macquart, 1840]; *appendiculata* (Macquart), 1849 (as *Lomatia*); *bivittata* Bezzi, 1925 (subg. *Pipunculopsis*); *hesperus* (Rossi), 1790 (as *Bibio*), *hesperus tropicalis* Bezzi, 1921 [= *albipectus* (Walker), 1849 (as *Anthrax*)]; *latifrons* Bezzi, 1924; *letho* (Wiedemann), 1928 (as *Anthrax*), *letho liliputiana* Bezzi, 1924; [= *longitarsis* (Becker), 1902 (as *Anthrax*)]; *sceliphronina* Séguin, 1935; *stenogaster* (A. Costa), 1884 (as *Anthrax*).

Ethiopian: *Petrorossia angustibasalis* Hesse, 1956, *angustibasalis buziana* Hesse, 1956; *chapini* Curran, 1927; *consobrina* Bowden, 1964; *deducta* Bowden, 1964; *flavicans* Bowden, 1964; *fulvipes* (Loew), 1860 (as *Anthrax*); *fumipennis* Hesse, 1956; *fuscicosta* Bezzi, 1924; *gratiosa* Bezzi, 1912; *imbutata* Hesse, 1956; *karooana* Hesse, 1956; *masienseensis* Hesse, 1956; *media* Séguin, 1931; *obscurior* Bowden, 1964; *phthinoxantha* Bowden, 1964; *plerophala* Hesse, 1956; *vinula* Bezzi, 1921.

Genus *Desmatoneura* Williston

FIGURES 133, 379, 636, 649, 908, 909, 910

Desmatoneura Williston, Kansas Univ. Quart., vol. 3, p. 267, 1895. Type of genus: *Desmatoneura argentifrons* Williston, 1895, by monotypy.

Small, rather slender flies with the abdomen tapered and longer than the thorax, tending to be a little compressed laterally and both thorax and abdomen covered with scattered, appressed, scaliform pile and longer, more erect pile along the sides of the thorax, pleuron, and sides of the abdomen. Closely related to *Aphoe-*

bantus Loew and *Euccesia* Coquillett, the venation is distinctive inasmuch as the second vein arises abruptly but not rectangularly at a distance in front of the anterior crossvein $1\frac{1}{2}$ to 2 times the length of that crossvein. Apically the marginal cell is swollen as rather more commonly seen in the South African genera of the *Aphoebantini*, but also present in some American *Aphoebantus* Loew. This apical swelling is due to an apical bend in the second vein. Another quite distinctive characteristic of *Desmatoneura* Williston is the striking, swollen and inflated front. The antennae are set at or slightly below the middle of the head in profile, hence the front is quite extended. The face is vertical, and there is a distinct transverse or curved fascia running midway between the antennae and the anterior edge of the oragenal recess. Finally, it may be added that the third antennal segment has the swollen basal part distinct from the short, apical styli-form part and the eyes are dichoptic in the male. Females always 2 or 3 times as large as the males.

Desmatoneura Williston as presently known is restricted to the arid region of the southwestern United States.

Length: 4 to 9 mm.

Head, lateral aspect: The head is subglobular, the occiput is short, and in the male of about equal length above and below, although at the middle of the posterior margin of the eye the occiput is a little more extensive because of the prominent, rectangular indentation of the eye margin accompanied by a short, horizontal, creaselike excision of the margin. In the female the upper occiput is a little longer than in the male, the lower occiput distinctly much shorter than in the male and the middle indentation along the eye margin deep, broad and angular but not rectangular. The pile of the occiput is quite short and minute and appressed near the eye margin but changes to a rather dense, moderately long fringe along the inner margin of the occipital recess. The front is distinctly swollen and inflated in both sexes in a characteristic fashion. And in the males it is completely covered with dense, silvery white, flat-appressed micropubesence directed forward and downward, extending from the ocelli to the antennae and out to the eye margin, among the micropubesence are a few, fine, scattered, erect hairs. In the females, however, the front is largely bare down the middle, shining, blackish in the type-species with some coppery reflection which appears to proceed from minute, scalelike elements and beginning in the middle of the front there are loose, appressed, scattered, scale-like hairs. In the females above the antennae and along the eye margins the ground color becomes yellowish and on the eye margins at least there is similar, minute, silvery micropubesence similar to that of the male. Also, the erect, scattered hairs are somewhat more numerous and extensive over the whole surface of the front, except linearly upon the eye margins. The face and front extend anteriorly forward from the eye a

distance nearly the length of the third antennal segment.

The circular, transverse fascia beneath the antennae is characteristic of this genus. The pile of the face consists principally of dense, fine, micropubesence with some additional, short, scattered, erect pile, more abundant in the male, and more abundant diagonally below each antennae. The fine fringe of facial pile extends as a fringe below the edge of the oral margin. The eye is large and extensive, quite hemispherical on the anterior half, the upper facets distinctly enlarged in the male. The proboscis is short, not longer than the oragenal recess, and not reaching to its apex either. It is rather thick and stout with a short, fleshy, muscoidlike development which bears a number of rather stiff hairs. The palpus is composed of one short, slightly swollen segment and a second, much clavate and apically swollen and rounded second segment, about 3 or 4 times as long as the first segment, and very narrowly attenuate and attached at its base. The first segment has minute micropubesence, the second bears similar micropubesence and laterally a few, short, stiff, bristly hairs. The antennae are attached at just below the middle of the head and are thrust strongly out laterally and are therefore much divergent apically. The first segment viewed from below is much longer than the second segment, viewed from above they are of about equal length and they are both short. Second segment with 3 or 4 long, stiff hairs dorsally. The third segment is bulbous at the base, rather abruptly narrowed on the lower half, less conspicuously on the dorsal part; the whole bulbar base not longer than the second segment of the antennae. The styli-form part of the third segment is thick and of about equal width and at the apex bears a short, blunt, conical microsegment. The first segment has a fringe of short pile laterally and ventrally.

Head, anterior aspect: The head is slightly wider than the thorax, almost circular from the front. In the male the eyes are separated by a distance equal the width between the antennae and in the female by twice this much distance. The antennae are separated widely by a distance rather greater than the length of the first two antennal segments. The ocellar tubercle is prominent, high, with vertical sides, small, the ocelli in an equilateral triangle. It is separated from the eye margin in the male and in the female separated on each side by almost the distance between the posterior ocelli. Anterior ocellus twice as large as the front ocelli. The oragenal recess is rather short, oval, comparatively shallow with sloping sides. From the front it is obliquely sloping and retreating backward. The genae are reduced to a mere line on the oragenal recess. The head viewed from the posterior aspect shows a very large, deep, occipital recess. Viewed from above the occipital lobes are separated by a distinct fissure behind the ocellar tubercle.

Thorax: The mesonotum is black, feebly shining, loosely covered with appressed, short, flattened scales or

hairs. There is a tuft of long, stiff, bristly hairs on the notopleuron and the scutellum has 2 pairs of long, slender, convergent bristles in the male, and in the female more numerous bristles. Disc of scutellum with similar scales to that of the mesonotum. The pleuron more or less yellowish or brownish, especially below; the mesopleuron has a conspicuous clump or band of stiff, pale bristles directed upward. Propleuron with a vertical fan of long, slender bristles directed outward. Whole surface of pleuron pollinose. The middle and lower mesopleuron and upper sternopleuron with appressed pile. Metanotum, metapleuron, and hypopleuron bare. There is, however, a tuft of flattened hairs immediately behind the spiracle and below the haltere.

Legs: The legs are slender, the middle and especially the hind pair much longer than the anterior legs. All of the femora plastered with closely appressed, small scales, rather more dense below. Anterior femur with a row of microsetae anteriorly, middle femur with 1 or 2 bristles anteriorly, hind femur with 4 or 5 sharp, stout, short, spinous bristles laterally on the posterior half and 2 or 3 others ventrolaterally and distally. Anterior tibia with 2 or 3 rows of minute, short setae; middle and hind tibia each with 3 rows of sharp, oblique, spinous bristles of no great length, and hind tibia with 4 rows of similar bristles. On the hind tibia these rows contain 8 to 12 bristles. Pulvilli long and slender, the claws sharp, slender and curved.

Wings: The wings are hyaline, the auxiliary cell and to a lesser extent the costal cell tinted. There are 2 submarginal cells. The anterior branch of the third vein arises obliquely but abruptly but never rectangularly. It is rather broadly rounded at the first bend and is strongly bent forward at the outer half. The second vein has an abrupt bend distally so that the apex of the marginal cell is widened. All the posterior cells are open, the anterior crossvein lies at or close to the basal fourth of the discal cell. The second vein arises very abruptly, in contrast to *Aphoebantus* Loew, but it is rounded and not rectangular. Anal cell widely open, alulae large, the ambient vein complete, the base of the wing with a hooklike spur. The second vein arises comparatively close to the anterior crossvein, removed from it by about $1\frac{1}{2}$ to 2 times the length of the anterior crossvein.

Abdomen: The abdomen is longer than the thorax, gently tapered posteriorly and more or less cylindrical. It is generally reddish or yellowish brown in color but tends to be obscurely blackish on the basal tergites, except laterally. The pile consists of rather loose, scattered, flat-appressed, rather long scales and flattened hairs. The first tergite, however, has a fringe of dense, erect, rather long, bristly hairs on the outer half. Male terminalia conical, triangular, moderately large and protrusive with inverted recess.

The male terminalia from dorsal aspect, epandrium removed, show a broad, short structure in which there is a wide, prominent, basally widened epiphallus with truncate, snoutlike apex. The basal part of the aedeagus

is extraordinarily large and bulblike. Dististyli flared outward like long, slender, undulate, apically pointed, leaflike structures. From the lateral aspect, these are also slender, undulate and pointed and the epiphallus is bifid. The large epandrium is elongate, yet triangular with rather strong, sharp, ventral lobe at the base. Basistylus also triangular and apically pointed.

Material available for study: I have before me a pair of the type-species given my by Dr. R. H. Painter. I have a series of individuals of the same species and one additional species collected by my wife, Marguerite Hull, and me the day after a heavy desert rain at Sells, Arizona. I also have a female I collected at Las Cruces, New Mexico.

Immature stages: Unknown.

Ecology and behavior of adults: These flies are found resting upon desert sand or soil and are often attracted to the edges of temporary ponds. I have never seen them upon flowers.

Distribution: Nearctic: *Desmatoneura argentifrons* Willison, 1895.

Genus *Chiasmella* Bezzi

FIGURES 378, 644, 654

Chiasmella Bezzi, The Bombyliidae of the Ethiopian Region, p. 156, 1924. Type of genus: *Chiasmella brevipennis* Bezzi, 1924, by original designation.

Medium-sized flies, rather similar in appearance to *Aphoebantus* Loew. The head is large and more or less globular, the posterior eye margin has a strong deep indentation. They are dark colored flies with fine grayish-white pollen and similar colored pile. They have hyaline wings and gently tapered abdomen.

The only known species is from Arabia.

Length: 11 mm.

Head, lateral aspect: The head is subglobular; the face is rather strongly produced, gently increasing to the oral margin; its height is nearly equal the length of the short antennae. The sides of the face have pollen above on the upper half, extending obliquely down to the eye margin; oral opening long but narrow, 4 times as long as wide. The eye has a prominent, deep indentation posteriorly, the occiput is tumid but chiefly swollen submedially, and it abruptly slopes to the eye margin where it is nearly plane with the eye. The middle of the occiput has a very large circular depression or bowl-like opening; there is a deep, medial fissure leading to the vertex; the pile is short, coarse, and flat-appressed but becomes erect, submedially along the rim of the opening. The palpus is short and concealed within the oral opening; the first segment is quite slender in comparison to the second, a little shorter, the second segment wide with more or less parallel sides, subtriangular in section and the apex rounded and bearing a number of rather short, bristly hairs apically, dorsally, and laterally. The short proboscis is extended forward, it bears

a few stiff hairs ventrally near the apex. The antennae are attached at the middle of the head and are short; the first two segments are quite short and nearly equal in length; the third segment is long, conical with nearly parallel sides on the attenuate distal third and bears 2 quite short, ringlike or annulate microsegments.

Head, anterior aspect: The front is slightly narrowed toward the vertex with scattered, flattened, appressed hairs; the ocellar triangle is quite small, situated just a little before the posterior corner of the eye; in the male the front is a little more narrow; it is about half the width of the female.

Thorax: With fine, scattered, suberect pile over the dorsum, which is rather short but this pile becomes a little longer laterally; along the anterior margin, it is more dense and appressed. The humerus is densely long pilose with a dense, long, pronotal collar of pile, coarse but nonflattened. The propleuron, laterally, and the whole upper half of the mesopleuron have dense, long, coarse pile. The sternopleuron dorsally and posteriorly, the posthypopleuron, and all the coxae have numerous, rather slender, whitish scales. The dorsal pteropleuron and the metapleuron have a rather dense patch of shorter pile; on the metapleuron it is curly. Squamae with a fringe of long pile. The scutellum is large, slightly thickened, convex along the margin, the disc and especially the margin with dense slightly flattened and flat-appressed pile; its margin has 2 or 3 pairs of slender, bristly hairs. The notopleuron has 1 long slender bristle, the postalar callosity has 3 pairs.

Legs: Slender; the femora and tibiae are covered with broad white scales. The hind femur has 5 or 6 short bristles placed laterally, and at the outer half, there are 6 ventrolateral bristles; hind tibia with 12 quite short, posterodorsal, 7 or 8 stouter anterodorsal, 5 or 6 anteroventral, and 6 or 7 posteroventral bristles. Middle femur with 5 anteroventral bristles; its tibia has 5 or 6 posterodorsal, 7 posteroventral, 4 or 5 anterodorsal, and a like number of anteroventral bristles. All the femora have scales. The anterior femur has a few short bristles; they are placed in the anteroventral and posteroventral, and the anteroventral position and are distributed along the middle; its tibia has 4 or 5 short, posteroventral bristles; pulvilli well developed; the arolium forms a minute short lapet.

Wings: The wing is hyaline. There are 2 submarginal cells and the first posterior cell almost maximally open, the anal cell narrowly open. The axillary lobe is narrow, the alula present but small, so that at the base the wing is about as wide as the wing apex. The anterior crossvein lies just beyond the basal third of the discal cell, and the second vein arises abruptly but rounded just before the anterior crossvein and removed from it by not more than the length of this crossvein. The discal cell is comparatively wide, with on the outer half the vein above and the vein below about equally convex and slightly narrowing the intercalary vein. The anterior branch of the third vein arises abruptly but plane and there is a strong backward bend in this vein, the

outer section plane; there is a similar subapical bend in the second vein. The ambient vein is complete.

Abdomen: With eight segments in the male, with dense, flat-appressed, flattened whitish pile on all of the segments which on the terminal part of the abdomen becomes almost scalelike. There is also a conspicuous lateral fringe of abundant, long, fine, white pile becoming a little shorter near the midline; the sternites are hidden by the curled tergite. The middles of the tergites on the second, third, and fourth segments have a blackish basal fascia that becomes a little wider in the middle.

Material studied: The type-species, a pair in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic (Arabia): *Chiasmella brevipennis* Bezzi, 1924.

Genus *Comptosia* Macquart

FIGURES 150, 156, 158, 209, 366, 424, 693, 735,
921, 922, 923, 924, 925, 926

Comptosia Macquart, *Diptères exotiques*, vol. 2, pt. 1, p. 80, 1840. Type of genus: *Comptosia fascipennis* Macquart, 1840, by monotypy.

Neuria Newman, *Entomologist*, vol. 1, no. 14, p. 220, 1841. Type of genus: *Neuria lateralis* Newman, 1841. Designated by G. H. H. Hardy, p. 54, 1922b. Edwards, p. 82, 1934, footnote, states: "I cannot trace an earlier selection of a genotype for *Neuria*; consequently Bezzi's 1924 reference to *pracargentata* as the genotype is invalid."

Alyosia Rondani, *Arch. Zool. Anat. Fisiol.*, vol. 3 (sep.), p. 54, 1863. Type of subgenus: *Comptosia maculipennis* Macquart, 1846. Designated by G. H. H. Hardy, p. 54, 1922b.

Alucosia Edwards, *Encycl. Ent.*, Paris, ser. B. II., Dipt., vol. 7, p. 95, 1934. Type of subgenus: *Neuria coraculum* Newman, 1841, by original designation.

Epidosina, new subgenus. Type of subgenus: *Comptosia vittata* Edwards, 1934.

White, in Hardy (1924), pp. 77-78, key to 18 species from Australia.

Edwards (1934), pp. 81-112, key to groups and description of 45 species.

Hardy (1941), pp. 223-225, key to 34 Australian species.

Large and sometimes very large flies ranging up to 56 mm. in wing spread. They are characterized by a relatively long, slender wing of comparatively uniform breadth in which the marginal cell is drawn backward and outward into a long, rounded, fingerlike lobe, sometimes called the radial loop, which cuts deeply into the first submarginal cell. Submarginal cells vary from 2 or 3, to occasionally 4 as in *Comptosia plena* Walker. Most species, however, have only 2 submarginal cells but the type-species has 3. A few species, moreover, have the wing narrowed toward the base with reduction of the axillary lobe. While a few species have the wings hyaline, the great majority of species have wings that are variously patterned with brown accentuated along the veins and crossveins and especially upon the fore-border of the wings and often leaving the apical fifth or the whole posterior border of the wings clear. Thus

the species fall into many pattern groups. In the type-species the wing is a uniform, beautiful, rufous brown in color extending nearly to the end of the marginal cell, appearing again at the apex of the wing and interrupted in the male by a transverse band of opaque white. Several species have the apex of the wing white or with preapical band. This band, more chalky in males, may be absent in females.

This complex of genera centering around the genus *Comptosia* Macquart has received a great deal of study by Edwards (1934), Hardy (1922, 1933), and Paramonov (1931), each of whom has made valuable and important contributions to our understanding of these genera. Because of the erratic, almost distorted, highly peculiar venation one is inclined to regard these flies as rather archaic; the loops and curves of the veins are probably mere specializations, but the extra crossveins suggest a condition that might have obtained a long time ago.

Rondani (1863) first attempted to subdivide the genus.

He restricted *Comptosia* Macquart to the species with 3 submarginal cells, and the antenna with a long style. He characterized *Macrocondyla* Rondani as having 3 submarginal cells and an indistinct antennal style. *Alyosia* Rondani was created for those species with 2 submarginal cells, and *Lyophlaeba* Rondani for the species with 4 submarginal cells. Because of misunderstanding of genera by several authors considerable synonymy resulted, which has been cleared by Edwards in his fine illustrated paper of 1934. Moreover, Edwards sought for and appears to have found other supplementary characters of considerable value. I have followed him to a large extent in this paper, but I have adopted *Lyophlaeba* Rondani as a genus for the South American forms because it has priority over *Macrocondyla* Rondani, and I have retained the latter only in a subgeneric sense.

Also, the abdomen is elongate oval, yet always considerably shorter than the wing. The pile of these flies is fine, short, and subappressed in most species but is somewhat long, erect, dense, and woolly in a few species; the majority have a strongly bare aspect.

The legs are slender and bear fine bristles on the hind femur. It should be noted that the proboscis varies from relatively short and stout with fleshy labellum, to others more slender in both respects but never greatly longer than the oral recess. The antennae are not greatly different from other Lomatiinae; the first segment is swollen and medially flared, generally a little longer and larger, and remaining segments much smaller. The face is short, the oral cavity strongly retreating.

The numerous species of *Comptosia* Macquart are restricted to Australia; the closely allied flies in the Chilean subregion fall in the related genus *Lyophlaeba* Rondani and the subgenus *Macrocondyla* Rondani; they differ from *Comptosia* Macquart by the presence of a large tuft of soft pile on the anterior metapleuron.

Length: 10 to 22 mm.; wings 10 to 56 mm.

The *Comptosia* Macquart complex of related genera and subgenera may be expressed in the following way: *Comptosia* Macquart: No pile in front of haltere and none on pteropleuron.

Comptosia Macquart in the strict sense: 3 submarginal cells; alula narrow; anal vein straight; radial loop deep; male costa tuberculate; wing near apex in male, sometimes female, with opaque white band. Type-species: *Comptosia fascipennis* Macquart, by monotypy.

Alyosia Rondani, subgenus: 2 submarginal cells; radial loop strongly developed and fingerlike. While either the distal crossvein, which breaks up the radial field into 4 submarginal cells, or the branch connecting the radial loop to the third vein (sectorial crossvein) may be regarded as a true supernumerary crossvein, I interpret the other veins in the radial field as being probable coalescent branches of the radius; I regard the whole *Comptosia* complex as constituting an apparently archaic relict group of bee flies which tend to reflect an early generalized venation. Therefore I leave *Alyosia* Rondani intact as a convenient name already in use. The presence of additional submarginal cells (Schiner, notwithstanding) is very useful in places within the family. The majority of genera have moved in the direction of a still more simplified venation, some even having the radial field reduced to a single submarginal cell. Type-species: *Comptosia maculipennis* Macquart, by designation of Becker.

Edwards (1934) presents no less than 4 species groups within this subdivision: *fasciata* Fabricius, *preargentata* MacLeay, *apicalis* Macquart, and the *ocellata* Newman group; 17 species included in all.

Epidosina, new subgenus. This name I propose for those species of the *Comptosia* complex with 4 submarginal cells. Radial loop strong and fingerlike. Anal vein straight. Axillary lobe wide and alula narrow. Type-species: *Comptosia vittata* Edwards.

Oncodosia Edwards. A genus distinguished by the large, very broad abdomen without prehalteral pile. Sides of abdomen with conspicuous flattened tufts of hair. Two submarginal cells present, except in occasional freakish individuals. Alula wide and large and anal vein sinuous. Wing characteristically very broad basally. Radial loop not extensive; commonly collected by Hull and his sons in Western Australia in 1954. Australian only. Type-species: *Anthrax patula* Walker, by original designation.

Alucosia Edwards, subgenus: Proposed by Edwards for those 15 species having the following ensemble of characters: three submarginal cells in the type-species, alula completely absent; wing markings of a different type, chalky white markings never present; second section of third branch of medius longer than or at least as long as the first, this

rarely true in *Comptosia* Macquart; the fourth branch of the radius more strongly recurved, the upturned part distinctly sinuous, rarely true in *Comptosia* Macquart. Type-species: *Neuria corculum* Newman, by original designation, contains 15 species.

Doddosia Edwards. A related genus with this ensemble of characters: Metapleuron with a conspicuous tuft of hair; pteropleuron bare in front of spiracle; distinct bristles present on middle and hind tibiae; abdomen with parallel sides; wings very broad, costal cell a little widened at base; venation essentially like *Comptosia* Macquart, the radial loop well marked; third posterior cell not narrowed at tip; anal vein straight; alula small. Type of genus: *Doddosia picta* Edwards. Found abundantly by Hull in northern Queensland.

However, I do not agree with certain earlier writers that the number of submarginal cells is of no significance whatsoever; we certainly find it invaluable in differentiating the species of *Ligyra* Newman (*Hyperalonia* of authors) from the more numerous forms of *Exoprosopa* Macquart; nor have I heard any one suggest abandoning it. I have retained the number of submarginal cells as part criterion for certain groups I recognize as useful subgenera, but I have superimposed this concept upon the pleural characters discovered by Edwards.

Head, lateral aspect: The head is globular with very strongly developed occiput, which, however, is steeply and convexly sloping to the eye margin down to the comparatively small but deep central cavity of the occiput. In some species the occiput is more extensive dorsally than it is below, in still others it is approximately equally extended dorsally and ventrally. However, in any case there is a characteristic, deep indentation at the middle of the posterior eye margin, with or without accompanying notch, but without bisecting line. The occiput is pollinose and the pile consists of minute hairs, more or less appressed or curled. There is an erect fringe of pile around the inner margin bordering the central occipital cup which varies from sparse to dense in different species. The front is convex, forming in males almost an equilateral triangle and extending about half the distance from the antennae to the posterior eye corners. This pile is erect or suberect, fine, bristly, and rather dense and in some species with subappressed, scaliform, glittering hairs. Typically there is a bare, narrow, foveal groove in the middle of the front which may be linear or as wide as an ocellus. It may extend as in the type-species, with crimped margin all the way between the antennae, or it may end in front of the antennae. In any case, however, there is a bare, triangular, or rhomboidal space in front of the antennae, bare of pile and containing pollen only. The front of the female is similar with pile a little more sparse.

The eye is quite large, slightly reniform, equally developed above and below, the upper and lower halves therefore symmetrical. The face in the male of the type-

species is not or scarcely at all visible in profile as it begins to recede from the upper margin of the antennae, and the oragenal cup likewise sinks below the eye margin, except at the bottom of the head near the base of the proboscis. This is likewise true of the female, except that the receding face is a little more extensive and visible beneath the antennae. The sides of the face bear dense coarse pile becoming shorter but extending down along the sides of the gena nearly to the base of the proboscis. The proboscis is stout, sometimes confined to the oragenal recess into which it is tucked. In other species it extends beyond the oragenal recess by one-third its length but when thrust upward, as it often is, it comes to rest between the antennae. In the type-species the proboscis is relatively short, and even with the fleshy lobes of the labellum apposed it would barely fit into the oragenal recess, and possibly a little beyond. In this species the labellum is short, broad, fleshy, with rugose or transverse channels much as in a muscoid. The two lobes are often divergent backward as large, more or less triangular flaps. The palpus is clearly composed of a short, basal segment, sometimes not longer than wide, again 2 or 3 times as long as wide, again 2 or 3 times as long as wide and with a long, slender distal segment, which bears numerous, fine, long, subappressed hairs. The apex is pointed, the whole segment cylindrical.

The antennae are attached near the upper third of the head. The first segment is strongly swollen, widened apically especially medially and also somewhat produced apically on the medial aspect, so that the apex is more or less obliquely truncate. Moreover, the first segment is rather strongly swollen and rounded below in the type-species and bears a tuft of rather long, oblique, bristly pile of the same length as the pile of the upper face. This segment is at least twice as long as its basal width and its apical width at least $1\frac{1}{2}$ times as long as its basal width. Thus, it appears to be somewhat flattened dorsoventrally and somewhat flared medially toward the apex. It is rather densely beset with stout, black, setate bristles on the whole medial surface, the dorsal surface, except at the base, and longer, finer bristles laterally proceeding chiefly from the basal half. The second segment is small, quite beadlike with rounded, convex sides medially and laterally; it is attached near the outer edge of the first segment so that the second and third segments diverge strongly. It has a few short setae dorsally. The third segment is more narrow than the second, widest at the base, rather strongly tapered to a point just before the middle from which the remainder of the segment is drawn out into a style of uniform thickness.

Head, anterior aspect: The head is circular and distinctly more narrow than the thorax. The eyes in the male vary from being almost holoptic and separated by only half the width of the ocellus, each upper eye contour being strongly rounded as in the case of the type-species, to others in which the eyes are separated by a little more than the thickness of the ocellus. In a

species before me the eyes are truly touching. In females the front is comparatively narrow and the eyes are separated at the vertex by a space sometimes as little as half the lower width of the front, and sometimes it is a little wider. The ocellar tubercle is never conspicuous, it has a clump of 8 to 20 long, fine, slender hairs curved forward and lying in a medial row and the ocelli occupy a short, isosceles triangle.

In the type-species the second antennal segment is as long as wide, in some species only half as long. The third segment in some species has the bulbous, basal part of the third segment much reduced in length, thus more sharply attenuate, leaving a proportionate, longer, slender, stylelike process on this segment. The antennae are separated at the base by a distance nearly equal the basal width of the first segment. From the anterior aspect the face is rather wide along the sides of the upper part but rapidly sinking down below the eye level near the upper third of the oragenal cavity. It continues to drop down into a long, narrow, deep, tentorial fissure which lies between the lower part of the oragenal cup and the genal part of the head.

The facial component may be considered to stop at the bottom of the facial slope. The whole sides of the face bear dense, long, somewhat oblique pile and the genal sides below along the eye margin bear a narrow fringe of pile. Walls of the oragenal cup folded inward near the middle. The head from the posterior view shows a strongly bilobed occiput with deep medial crease extending almost to the vertex in the type-species, in other species only half the dorsal length of the occiput.

Thorax: The thorax is short and compact, rather strongly widened posteriorly, the posterior width of the mesonotum is as great as its length, and the humeri extend outward behind as a transverse, vertically flattened lobe. The mesonotum is densely pollinose and in some species feebly shining. It is comparatively low and only gently convex, equally convex in front and behind. The pile consists of dense, short, oblique, very fine, bristly hairs arising from minute tubercles in some species; in others the fine hairs are longer, erect, and without tubercles. In still other species it is composed of coarse, flat-appressed, pale hairs intermixed with extraordinarily fine, erect, black hairs. Pile of scutellum similar to that of the mesonotum. The humeri have dense pile also similar to the mesonotum. Notopleuron with 3 or 4 and postalar callosity with 1 or 2 stout, rather long bristles, pale in color. Scutellar margin usually only with long, bristly hairs. The scutellum is large, distinctly subtriangular with the apex rounded, the pollen thin, and the whole scutellum flattened toward the apex.

The pleuron is pollinose; the upper half of the mesopleuron bears dense pile, which is fine, bristly and curled and extending upward. The upper sternopleuron has a little fine pile but the pteropleuron and hypopleuron and metapleuron in front of the spiracle are all bare. The lateral metanotum bears a conspicuous

band of long pile, generally pale, with some black hairs intermixed, and there are a few hairs on the posterior metapleuron above the hind coxa. The propleuron has tufts of long pile. Prosternum with long pile; the alary squama is short but bears the usual *Lomatia*-like, wide, plumose band of pile. The halteres are relatively small.

Legs: The legs are well proportioned to the body without being large. The first 4 femora are slightly enlarged over the middle and base, the hind pair stout without being large. The femora vary from black to yellow or red, with the tibia always pale. The anterior femur of the type-species is covered with minute, flat-appressed, setate hairs and 4 or 5 spines anteroventrally. On the middle pair the pile is similar, but somewhat larger, and the bristles of the same number, and on the hind femur in addition to the small, flat-appressed hairs, there are 7 short, setate bristles anterodorsally on the outer half, and on the whole anteroventral length of the hind femur there are 12 somewhat longer, oblique, stout, black bristles, and in a few species even more. In others there are a few slender bristles restricted to the outer half. In some species of *Comptosia* Macquart the anterior 4 femora have scattered, fine, long, erect, bristly hairs on the posterior surface and they may lack bristles on the anterior femur and the pile of the posterior femur may be rather matted and scalelike.

Anterior tibia anteroventrally with a dense brush of appressed, golden setate pile in the type-species and a similar brush of darker color in blackish species. The spicules or bristles of the anterior tibia are small, fine and in some species scarcely differentiated. In the type-species there are 3 anteriorly, 5 or 6 posterodorsally. Other species have 8 to 10 anterodorsally, 6 to 8 posterodorsally, and a like number posteroventrally. The middle tibia has 4 rows of bristles of variable length and stoutness. The anterodorsal row has 7 to 10; the posterodorsal row has 8 to 12; the posteroventral row has 3 to 8; and the anteroventral row has 6 to 12. Hind tibia likewise with 4 rows of bristles of about the same numbers. Tarsi short, strongly spiculate below, except that there are none upon the anterior tarsi, and only 1 row upon the hind tarsi. Claws and pulvilli usually small, the latter extending to the end of the claw with rounded apex. In the type-species the claws and pulvilli are quite large, the former rather slender but strongly curved at the apex, the wide spatulate pulvilli are rather truncate at apex, and with the arolium rather large, but smaller in other species.

Wings: The wings are elongate, slender in most species but in some species as in the type-species, they are extraordinarily long and slender. Wing patterns fall into several groups; in the type-species it is a uniform, beautiful, reddish brown throughout in the females, similarly colored but with a conspicuous, opaque, chalky white, preapical band in males. This preapical band is characteristic of a number of species in this genus. Some equally large species have the veins of the

wing diffusely margined with dark brown, the interior of the cells lighter. Still a third group of species have the anterior half of the wing dark brown without pre-apical spots. The posterior border of the brown color is irregular, usually filling all of the first and part of the second and third basal cells and cutting across cells to the apex. This group of species tends to have the wings strongly narrowed toward the base. The axillary lobe is extremely narrow, especially basally, and the alula absent or nearly so (subgenus *Alyosia* of Edwards).

In all members of the genus the radial loop is long and fingerlike, the marginal cell greatly extended downward, the end of the second vein strongly recurrent. All 4 posterior cells are open, the anal cell is widely open, the anal vein nearly straight, never bowed backward, and the anterior crossvein enters the discal cell at the outer seventh or outer eighth of the discal cell. Costal margin denticulate in the males of some species including the type-species, and there is a prominent, precostal, triangular nodule or spur. The alula in *Comptosia* Macquart ranges from narrow with a plane margin to species where it is absent; the ambient vein is complete.

Abdomen: The abdomen varies from species where it is short oval, basally as wide or wider than the width of the thorax behind the wings, to other species where it is more elongate, $1\frac{1}{2}$ to 2 times as long as the thorax and with the lateral margin nearly plane, the whole abdomen tapered. In males I find 8 tergites with the ninth forming a medially notched shield placed dorsally over the small and quite recessed terminalia. In the type-species the eighth and ninth male tergites are likely to be completely recessed beneath the seventh, the last sternite likewise recessed; ninth male tergite bilobed; in some males there appear to be 10 tergites. In females I find 8 tergites with the female terminalia recessed within a posterior pocket and surrounded by strong, bristly hairs. Postmargin of last sternite always plane.

The abdomen of *Comptosia* Macquart is usually blackish; in the type-species, however, it is brownish red laterally with the broad, medial, black, continuous vitæ becoming narrower posteriorly and extending outward along the posterior margin laterally but never reaching the corners. The pollen of the abdomen is generally faint but may be thick and dense, often leaving the abdomen shining. The abdominal pile consists of scattered, fine, short, largely appressed, bristly hairs, or with similar, even finer hairs erect and extending upward over disc and lateral margin, and with a variable amount of fine, short, curled, pale, flat-appressed hairs generally concentrated along the posterior margin and more sparse on the anterior part of the tergites. Anteriorly the lateral border of the first tergite shows a brush of erect, unusually fine hairs, not coarse and spikelike as in other genera. It may extend all the way across the segment and in a few species forms a narrow, complete band of bushy, tangled pile

on the posterior border of this tergite. Oddly enough, some species have only a few hairs basolaterally on the first tergite.

The male terminalia from dorsal aspect, epandrium removed, show an elongate figure with more or less parallel sides much as in *Lomatia* Meigen. Here again the dististyli are either leaflike viewed from above or twisted outward; in any case they are stout and blunt. The epiphallus and aedeagal complex are long and spoutlike. Basistylus elongate and dorsally ventrally widened apically.

Material available for study: In my own collection there are about 20 or more species, many of them collected by the author and his sons while in Australia in 1953 and 1954, in both the eastern and western sections of the country. I have also studied the material in the collection of the Commonwealth Scientific and Industrial Research Organization at Canberra, through the courtesy of Dr. A. J. Nicholson and his associates, especially Dr. S. J. Paramonov. I have also had the advantage of studying the material in the British Museum (Natural History) and in the United States National Museum (now National Museum of Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: These flies commonly feed on various species of the genus *Leptospermum*, a flowering genus of the family Myrtaceae, ranging from low, herblike forms to shrubs and small trees; few plants attract Diptera in such quantities or such great variety. At Canberra I collected a series of the beautiful type-species on these flowers.

Distribution: Oriental: *Comptosia indecora* (Wulp), 1885 (as *Neuria*).

Australian: *Comptosia albofasciata* Thomson, 1869; *angusta* Edwards, 1934 (subg. *Aleucosia*); *apicalis* Macquart, 1848; *atherix* (Newman), 1841 (as *Neuria*) (subg. *Aleucosia*) [= *geometrica* Macquart, 1847]; *aurifrons* Macquart, 1849; *bancrofti* Edwards, 1934; *basalis* (Walker), 1849 (as *Anthrax*); *bicolor* Macquart, 1849; *biguttata* Edwards, 1934; *brunnea* Edwards, 1934; *calophthalma* Thomson, 1869 (subg. *Aleucosia*); *cineta* Edwards, 1934 (subg. *Aleucosia*); *coraculum* (Newman), 1841 (as *Neuria*) (subg. *Aleucosia*); *costalis* Edwards, 1934 (subg. *Aleucosia*); *cuneata* Edwards, 1934 (subg. *Aleucosia*); *decedens* (Walker), 1849 (as *Anthrax*); *dorsalis* (Walker), 1849 (as *Anthrax*) (subg. *Aleucosia*); *edwardsi* Hardy, 1941; *extensa* (Walker), 1835 (as *Anthrax*); *fasciata* (Fabricius), 1805 (as *Anthrax*) [= *ignescens* (Newman), 1841 (as *Neuria*)]]; *fascipennis* Macquart, 1840; *fulvipes* Bigot, 1892 (subg. *Aleucosia*); *gemina* Hardy, 1941, [= n.n. for *cognata* Walker, 1852 (as *Anthrax*) not *cognata* Walker, 1849]; *hemiteles* (Schiner), 1868 (as *Neuria*) (subg. *Aleucosia*); *inclusa* (Walker), 1849 (as *Anthrax*); *lateralis* (Newman), 1841 (as *Neuria*) [= *ducens* (Walker), 1852 (as *Anthrax*); = *grandis* (Schiner), 1868 (as *Neuria*)]]; *rufoscutellata* Jaenicke, 1867; *maculipennis* Macquart, 1846 (subg. *Alyosia*); *maculosa* (Newman), 1841 (as *Neuria*) (subg. *Aleucosia*), [= *fulvipes*,

Bigot, 1892]; *moretonii* Macquart, 1855; *murina* (Newman), 1841 (as *Neuria*); *obscura* (Walker), 1852 (as *Anthrax*); *ocellata* (Newman), 1841 (as *Neuria*); *partita* (Newman), 1841 (as *Neuria*) (subg. *Aleucosia*); *plena* (Walker), 1849 (as *Anthrax*) (subg. *Aleucosia*); *prae-argentina* (MacLeay in King), 1828 (as *Anthrax*); *quadripennis* (Walker), 1849 (as *Anthrax*); *rubrifera* (Bigot), 1881 (as *Ligyra*); *sobria* (Walker), 1849 (as *Anthrax*); *serpentiger* (Walker), 1849 (as *Anthrax*) (subg. *Aleucosia* Edwards); *stria* (Walker), 1849 (as *Anthrax*); *sylvana* (Fabricius), 1775 (as *Bibio*); *tendens* (Walker), 1849 (as *Anthrax*); *tricellata* Macquart, 1847 (subg. *Aleucosia*); *tripunctata* Edwards, 1934 (subg. *Aleucosia*); *ritata* Edwards, 1934; *walkerii* Edwards, 1934; *williamsi* Edwards, 1934; *insignis* Walker; *subsenex* Walker.

Genus *Lyophlaeba* Rondani

FIGURES 147, 151, 154, 157, 161, 162, 368, 656, 673, 988-993

Lyophlaeba Rondani, Arch. Zool. Anat. Fisiol., vol. 3, p. 55 (sep.), 1863. Type of genus: *Lyophlaeba lugubris* Rondani, 1863, by original designation; 1 species.

Macrocondyla Rondani, Arch. Zool. Anat. Fisiol., vol. 3, p. 55 (sep.). *Macrocondyla* Rondani is regarded in this work as a subgenus of *Lyophlaeba* Rondani. 1863. Type of subgenus: *Macrocondyla pictinervis* Rondani, 1863, by original designation; 1 species.

Triloncra Schiner, Verh. zool.-bot. Ges. Wein., vol. 17, p. 312, 1867. Type of genus: *Comptosia lugubris* Philippi, 1865, by monotypy.

Liophlcha Bezzi, The Bombyliidae of the Ethiopian Region, p. 4, 1924, emendation.

Compssella, new subgenus. Type of subgenus: *Macrocondyla transandina* Edwards.

Paramonov (1931), pp. 1-218, treatment of *Lyophlaeba* Rondani, including *Macrocondyla* Rondani.

Edwards (1934), pp. 103-110, treatment of *Macrocondyla* Rondani and *Lyophlaeba* Rondani.

Paramonov (1948), pp. 146-148, key to 19 species (including *Macrocondyla*), from Bolivia, Chile, and Patagonia.

Large flies with comparatively long, tapered, flattened abdomen bearing generally a medial vitta or series of medial spots and pile generally of two types, with very fine, erect, black hairs and soft, matted, appressed tufts of pale pile outlining the tergites; these tufts are sometimes lacking.

Adopting the principle of the first reviser of the group, we have followed Paramonov (1931), and so we subordinate *Macrocondyla* Rondani as a subgenus of *Lyophlaeba* Rondani. We accept *Lyophlaeba* Rondani for all of the South American species related to *Comptosia* Macquart because of this principle; this prevents the matter of priority being a question for future consideration. Because the number of submarginal cells in these and related flies is stable within the species, I cannot agree that it is without value; coupled with the characteristics of the antenna and the pleuron, it forms a useful character for the division of *Lyophlaeba* Rondani into subgenera. Edwards (1934) noted that all the flies in this genus have a large, dense tuft of pile on

the anterior metapleuron, much similar hairs on the pteropleuron, third posterior cell not marginally narrowed, radial loop prominent, anal vein straight, axillary area moderately large, alula small with plane margin. The eyes of the male are either narrowly separated or almost touching. Edwards (1934) proposed treating *Lyophlaeba* Rondani as a subgenus. Paramonov considered that *Lyophlaeba* Rondani should take precedence over *Macrocondyla* Rondani, and we have decided to follow Paramonov for the reasons given above. The type-species of subgenus *Macrocondyla* is *pictinervis* Rondani. I divide the genus as follows:

The genus *Lyophlaeba* Rondani, with type-species *lugubris* Rondani, has 4 submarginal cells. The first antennal segment is long, without medial hair tuft at apex. Third antennal segment quite long, not styliform apically, in males shaped like a sword with a curved blade, in females more plane; apex bifid, the short spine articulated and dorsal and subapical. The proboscis is long and pulvilli are quite rudimentary.

The subgenus *Macrocondyla* Rondani has 3 submarginal cells. The first antennal segment is widened medially at apex and has a conspicuous tuft of long pile; third antennal segment strongly attenuate with minute spine at apex. Pulvilli conspicuous, more than half as long as claw. Wings clouded or banded.

Compssella, new subgenus, with 4 submarginal cells and first posterior cell divided by a crossvein. Type of subgenus: *Macrocondyla transandina* Edwards. These would be the least simplified in terms of venation and presumably the oldest of the group. Radial loop long, wing mottled and banded.

This genus with its subgenera is entirely South American and almost restricted to the Chilean subregion.

Length: 13 to 22 mm.; of wing, 12 to 22 mm.

Head, lateral aspect: The head is subglobular, the occipital component very prominent on the upper half and from the eye margin rounded and sloping backward leaving the occipital cup small but deep, and the marginal fringe of the recess dense but short. The upper half of the occiput varies from species in which it is shining, and uncommonly without pollen, to most species where the pollen is dense. The pile on this part of the occiput is rather scanty, consisting of short, stiff hairs curled and appressed forward and not reaching the eye margin. This condition extends to the bottom of the eye, or lower. The front in males is triangular and pollinose and in both sexes covered rather densely with shaggy pile appressed downward. From the lateral aspect both face and front are quite short, not extending beyond the eye margin. The face bears dense, long pile laterally in considerable amount and the whole surface is pollinose. The eye is kidney-shaped with deep but broad indentation a little below the middle, the indentation is equal in angle, above and below its greatest indentation. The proboscis is elongate and slender with very small labellum, often thrust obliquely downward, but in the resting position it extends obliquely up between the antennae. It is shortest in those species of the

subgenus *Macrocondyla* Rondani, sensu stricto. Generally the proboscis extends well beyond the head and antennae. Palpus slender and elongate, composed of a short, somewhat fused basal segment and a much longer apical segment. The palpus bears a number of long, fine hairs.

The antennae are attached at the upper third of the head, the first segment is large, much swollen, barrellike but not greatly asymmetrical. It is 4 or 5 times as long as the much smaller, much more narrowed, beadlike second segment. Third segment nearly as long as the first two segments together but sometimes a little shorter. It may be flattened, lanceolate, and leaflike, or cylindrical and tapering on the outer third where it is much more narrow. Apically it bears a small, stubby, minute spine.

Head, anterior aspect: The head is circular, not quite as wide as the thorax at its greatest width. The eyes in the male are narrowly separated, sometimes by as little as the width of one ocellus, sometimes slightly more. The ocellar tubercle is set almost at the posterior eye corner, is rather low, and the lateral ocelli touch the eye margin in the males. The front forms an almost equilateral triangle, and the vertex is extended forward in front of the ocelli with nearly parallel sides for an additional distance rather greater than the length of the ocellar triangle; this triangle is isosceles in shape. In the females the eyes are separated at the vertex by a distance equal 3 times the space between the ocelli. In both sexes the front is densely pollinose with a narrow, bare, longitudinal, foveate depression extending from the vertex and widening immediately in front of the antennae and extended as a tongue-like, triangular extension between the antennae. The antennae are separated quite widely in some species, enough for the proboscis to fit between them. The oragenal opening is quite wide below reaching almost to the eye margins but strongly and progressively narrowed anteriorly, ending immediately beneath the antennae. The walls of the oragenal recess are thick and inflated, except near the bottom of the eye where they become much thinner, and the recess is much deeper. However, this recess is quite deep throughout the lower four-fifths, becoming shallow only a short distance from the antennae.

Moreover, the tentorial fissure is wide and extremely deep, so that at no great distance from the antennae this fissure begins and leaves the head adjacent to the eye margin itself, shelving deeply inward. It ends at the beginning of the gena which extends deeply beneath the eye. Anterior genal margin polished and bare. The head viewed from above shows that the very extensive occipital lobes are tightly apposed behind the vertex.

Thorax: The thorax is longer than wide, widest posteriorly; the mesonotum is low and quite gently convex, its pile consists of dense, fine, rather short, slightly appressed hairs both pale and black and in some species vittae of flat-appressed, straggly, dully white, tangled hairs. The more erect, bristly hairs, though fine, tend to be longer on the posterior third of the mesonotum and

in front of the scutellum. There is a well-developed anterior collar of stiff pile on the mesonotum which extends over and includes the prominent humeri. The latter have a posterolateral blunt spur. Scutellum large with circular, posterior margin somewhat flattened apically, the pile similar to the mesonotum, with weak, long bristles on the margin and sometimes laterally. Notopleuron with 4 or 5, and postalar callosity with 5 or 6 bristles, which are rather stout and conspicuous. Pleuron pollinose with a conspicuous tuft of fine, tangled, and radiating pile and some bristles on the upper half of the mesopleuron; these may extend more loosely over the whole pleuron. The sternopleuron is more than usually pilose, the whole upper half has a bushy mass of dense, long pile appressed downward. In a few species the quantity is reduced. Propleural and prosternal pile extensive and long. The metanotum is both pilose and bristly. Both the anterior metapleuron in front of the haltere and the posterior metapleuron behind the spiracle have conspicuous tufts of rather dense, long, fine pile. Hypopleuron bare. Halteres small. Alary squama short but with dense, plumelike fringe. Pteropleuron without pile.

Legs: The legs are well developed. Anterior and middle femora slightly but distinctly swollen from the apex to the base. Hind femur stout without being swollen. All the femora have flat-appressed pile, sometimes fine, black and setate, on others pale, shining and scaliform, and in some the pile is a mixture of these two types. The appressed scaliform pile is more common. Anterior femur with a few very fine, erect hairs below and generally with 4 to 7 slender, anteroventral bristles. Middle femur with 4 or 5 much stouter, sharp, anterior bristles and the hind femur characteristically with 6 to 8 prominent, rather long, slender, black, anteroventral bristles, and 4 or 5 anterodorsal setae on the outer half. The anterior tibia is shorter than the middle tibia, the middle tibia nearly if not quite as long as the hind tibia. Anterior tibia with distinct, bristly spicules; there are 5 or 6 anterodorsal ones, 8 to 10 anteroventral, sometimes 6 to 8 additional bristles between, 10 to 12 smaller, posterodorsal ones, and 8 to 10 posteroventral ones. Lower surface of anterior tibia with a slender brush of dense, appressed setae. Middle tibia with 4 rows of bristles; 8 to 10 anterodorsally, about the same number of posterodorsal bristles which are rather smaller and about 10 posteroventral bristles, and there are 5 or 6 anteroventral bristles. Hind tibia with well-developed bristles, all of them short, the dorsal bristles a little stouter. There are 10 to 12 anteroventral ones, the same number of anterodorsal ones, and 4 to 7 posterodorsal bristles, and 7 to 10 posteroventral bristles.

Anterior tarsi quite short without spicules below, remaining tarsi, however, strongly spiculate ventrally. Claws slender, sharp, and strongly curved apically, and with a long pulvillus which is quite slender. There is a short, triangular arolium.

Wings: The wings are long and slender, longer than the abdomen. There are 3 submarginal cells, except in

the genus *Lyophlaeba* Rondani, which has 4. The subgenus *Macrocondyla* has a woolly, densely pilose mesonotum and abdomen and the first posterior cell almost closed. Wing with a strong brown pattern somewhat diffuse, darker on the basal third of the wing in front of the second basal cell. The brown pattern runs down each side of the cubital vein, as a spot across the anal vein and with a second concentration of brown color subapically across the wing, leaving the veins widely margined with brown; the centers of the cells more or less diffusely hyaline; in some species, as in *Lyophlaeba lugubris* Philippi, almost the whole wing is brown with very faint, subhyaline spots in a few cells. The radial loop is prominent, although its extent varies. The first posterior cell is more strongly narrowed than in *Comptosia* Macquart. The anterior crossvein enters the discal cell from the outer fourth to the outer sixth. Alula short and linear. Costa widened at the base with a basal, costal spur. Margin of the costa never denticulate.

Abdomen: The abdomen is elongate, distinctly longer than the thorax, rather strongly flattened and long conical or slightly oval in shape. I find 9 tergites in the male, the last one forming a short hood over the small recessed genitalia. In the females I note only 7 tergites, any others being completely recessed. The pile of the abdomen varies from dense, matted, fine, short, flat-pressed, pale pile among which there is considerable amount of longer, quite fine, bristly, black pile over the whole tergite, and curled obliquely backward. The pale pile in some species is restricted to narrow, posterior borders, and in some species there is similar, matted, appressed, slightly longer pile forming a continuous vitta or stripe down the middle of the abdomen and again narrowly along the lateral margins. The erect, bristly pile tends to be a little stouter along the lateral borders, but there are no banked, flattened tufts of lateral pile. Lateral third of the first tergite usually with a rather dense brush of erect, coarse pile.

Material studied: I have 5 species, including several sent to me by Alfredo Faz from Chile in 1923 and also the type-species.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no record of the flowers these flies frequent.

Distribution: Neotropical: *Lyophlaeba argentinae* Paramonov, 1940 (as *Lyophlaeba*); *bifasciata* (Macquart), 1849 (as *Comptosia*); *bigoti* Edwards, 1934; *blanchardi* Paramonov, 1931 (as *Lyophlaeba*) [= *bifasciata* Blanchard, 1852, not Macquart]; *boliviana* Paramonov, 1931 (as *Lyophlaeba*); *canescens* Philippi, 1865; *chilensis* Paramonov, 1931 (as *Lyophlaeba*); *consobrina* (Philippi), 1865 (as *Comptosia*); *edwardsi* Paramonov, 1948 (as *Lyophlaeba*) [= *montana* Edwards, 1934, not Philippi]; *haywardi* Edwards, 1934; *infumata* (Philippi), 1865 (as *Comptosia*); *koslovskiyi* (Edwards), 1934 (as *Ligyra*); *landbecki* (Philippi), 1865 (as *Comptosia*); *lugubris* Rondani, 1863 [= *lugubris* (Philippi), 1865 (as *Comptosia*)]; *manca* Edwards,

1934; *minuta* Paramonov, 1931 (as *Lyophlaeba*); *montana* (Philippi), 1865 (as *Comptosia*); *pallipennis* Paramonov, 1940 (as *Lyophlaeba*); *parbifasciata* Paramonov (as *Lyophlaeba*), 1940; *philippii* Paramonov, 1931 (as *Lyophlaeba*) [= *bifasciata* Philippi, 1865, not Macquart]; *picinervis* (Rondani), 1863 (type of subgenus: *Macrocondyla*), [= *vulgaris* (Philippi), 1865 (as *Comptosia*)]; *setosa* Paramonov, 1940 (as *Lyophlaeba*); *transandina* Edwards, 1934.

Genus *Ylasoia* Speiser

FIGURES 148, 367, 659, 670, 985, 986, 987

Ylasoia Speiser, Zool. Jahrb., Jena, vol. 43, p. 213, 1920. Type of genus: *Anthrax pegasus* Wiedemann, 1828, by original designation.

Long-winged, black-winged flies of medium size in which there are 2 irregular hyaline crossbands on the wing, one near the base, one near the apex, in addition the middles of some posterior and apical cells are faintly paler; the color of the wing is much blacker than commonly seen. There are only 2 submarginal cells and the radial loop is long. There is a faint, narrow, gray, medial vitta down the abdomen, a similar one on the mesonotum besides on each side a sublateral, wider, orange vitta.

The occiput is very long and bilobate above, the third antennal segment long and attenuate, the proboscis very short, quite stout with large muscoidlike labellum.

The pteropleuron bears a tuft of hair posteroven-trally and there is a small tuft on the metapleuron behind the spiracle but none in front. Lateral metanotum bristly.

The most distinctive character of this genus apart from the patch of pile on the pteropleuron lies in the third posterior cell which marginally is greatly narrowed.

Three species have been assigned to this south Neotropical genus; two of them may perhaps be subspecies. Males have the hyaline areas more reduced and the second hyaline band more of a chalky white. The affinities of the genus seems to be nearer the Australian genus *Oncodosia* Edwards, than to the South American genera like *Lyophlaeba* Rondani.

Length: 10 to 12 mm., of wing 13 to 15 mm.

Head, lateral aspect: The head is hemiglobular with the occiput on the upper part of the head and unusually reduced below. The occiput is thinly covered with brown pollen, the pile consists of abundant but not dense, fine, quite short, erect, black setate hairs, curved a little forward and extending to the eye margin. The eye is kidney-shaped, very deeply indented, the lower angle much more acute than the upper angle. There is a small, impressed rim behind the eye on the upper half. Central fringe of the occipital recess short and scanty, the cavity unusually large. The front is flattened, except on each side in front of the antennae, where it is slightly raised. Pile abundant but not dense,

moderately long, fine, erect, and black. The face in lateral aspect is not at all produced and is scarcely visible.

The proboscis is short, stout, and robust but with an exceptionally large, fleshlike labellum, the inner surfaces of which have transverse grooves. The labellum is at least as long as the basal part of the proboscis; it does not reach quite to the antennae. Palpus stout with a short basal segment more or less fused to the slightly longer clavate, apical segment. The latter bears a few ventral hairs. Antennae attached a little above the middle of the head, they are elongate, the first segment stout but much more slender than in related genera; they are slightly widened at the apex medially and bear apically at the outer edge a small, short, beadlike segment. First segment with numerous appressed, fine bristles and bristly setae above and much longer, appressed, coarse, black bristly pile below. Second segment with fine setae on all sides. Third segment at the base no wider than the second segment, slightly widened just beyond the base, then gradually tapered to near the apex where the thick styloform portion has parallel sides and bears a small, short spine. The third segment is slightly longer than the first two segments combined.

Head, anterior aspect: The head is circular, as wide as the thorax, the eyes in the females are separated at the vertex by about twice the width of the ocellar triangle. Ocellar triangle short isosceles; the tubercle is a little raised and bears fine, moderately long, black hairs similar to that of the front. Whole front sepia brown pollinose. Antennae rather widely separated at the base with a triangular, tongue-like extension of the front between the antennae. The oragenal recess is wide but rather shallow. It extends to and between the antennae, and is deeper posteriorly. The lower sides of the face shelve inward almost vertically beginning on the lower third of the eye. The tentorial fissure is quite deep and the lower wall of the oragenal recess quite thin, and not extending upward to the level of the eye. Sides of the face throughout with a few scattered, long, fine, erect hairs. Gena small and narrow and neither occiput nor gena at all extensive below the eye. The occiput viewed from above shows the lobes to be quite tightly apposed with a punctate depression in front of the fissure and behind the ocellar tubercle; the latter extends a short distance behind the posterior eye corners, which are, however, rounded forward.

Thorax: The thorax is dark brown with clay colored pollen on most of the pleuron and remaining pleuron with darker pollen. The thorax is wider posteriorly, the mesonotum low, slightly convex posteriorly and anteriorly, flattened before the scutellum and without any intermediate fissure. The mesonotum is black with pale, strikingly colored vittae of quite dense pollen, besides a median, linear, gray vittae there are 2 widely separated, rather wide, posteriorly divergent, bright, brownish yellow vittae running from the anterior margin and disappearing in an area of brown pollen just

before the scutellum. In between and on each side of these yellow vittae there are 3 black stripes bearing very dark pollen, and the lateral margin is light brown. The pile of the mesonotum consists of scanty, fine, erect or suberect hairs of no great length, but the anterior mesonotal collar consists of spikelike black, erect bristles extending over the humerus, especially anteriorly. The humerus is large and swollen, with the posterior surface high and vertical and bearing a posterolateral tubercle. Notopleuron with 2 stout, long bristles. Postalar callosity with 2 long bristles and a few bristly hairs. Scutellum large, the posterior margin evenly rounded, the whole opaque black, the sparse discal pile like that of the mesonotum but longer, the margin with numerous, longer, slightly stiffer bristles and a little short, curled, yellow pile. Whole mesopleuron pilose with scattered, fine, erect, shining black hairs becoming slightly bristly above. Upper sternopleuron with a few similar, appressed hairs. Metapleuron in front of the haltere without pile but metapleuron behind the spiracle with a tuft of 10 or 12 hairs and the posteroventral pteropleuron with a tuft of about 25 long, erect, slender, bristly hairs. Hypopleuron without pile. Squama with a wide band of pile but very loose and bristly in character. Halteres long, the elongate club flat.

Legs: The legs are stout, the anterior coxa quite long, three-fourths as long as the anterior femur. All the femora have appressed, shining, blackish setae and a scanty fringe of fine hair below. Anterior femur shorter than the middle one and the middle one shorter than the third femur. The femur bears conspicuous, sharp, stout, rather strongly appressed, anteroventral bristles. They vary somewhat in numbers but there are usually 6 or 7 present. Other femora with at most 1 or 2 bristles, sometimes none. Anterior tibia stout with appressed setae and with rather well developed, short, oblique bristles. There are 10 or 12 anterodorsally, 10 slightly longer ones posterodorsally, 8 posteroventral, and 6 or 8 ventral or anteroventral. Middle tibia similar, the bristles slightly longer and slightly stouter, and with 5 rows, the anterodorsal row with 14, the others 6 to 8. Hind tibia similar, the bristles slightly longer, and with 4 rows, the anterodorsal row with 10, the dorsomedial row with the same number, the ventromedial row with 5, and the anteroventral row with 5 bristles. Tarsi long but stout, strongly spiculate below. Claws sharp, strongly arched, pulvilli long, rather broad and the arolium long.

Wings: The wings are rather broad but long, much longer than the abdomen, somewhat narrowed at the base, in part hyaline but more extensively blackish. The black color is due to very dark, sepia brown coloration, and dark brown villi, and appears even blacker because of the dense, nearly white villi of the sharply contrasted pale bands and spots. There are only 2 submarginal cells. The radial loop and prolongation of the marginal cell is extensive. The first posterior cell is narrowed apically, the third posterior cell is equally

narrowed apically, and the anal cell is as widely open as both these posterior cells. The anterior crossvein enters the discal cell at the outer sixth, the axillary lobe is narrow, the alula wanting, the ambient vein complete. There is a continuous, pale, vertical stripe across the wing on the outer third, some small, diffuse, pale spots in the centers of most cells, a large, elongate, pale spot just before the apex and lying in the outer half of the second basal cell. There is a larger spot occupying the whole of the middle of the anal cell, continued across the anal vein in wider extent to occupy the middle of the axillary lobe.

Abdomen: The abdomen is elongate oval and in the middle wider than the thorax. It is opaque black with dense, very dark brown pollen, becoming greenish when viewed from the rear and with a narrow, medial vitta down the abdomen composed of confluent, wedgelike spots of pale brownish or greenish-yellow pollen. Pile of the abdomen scanty, fine, black, suberect, bristly in character. There is similar pile a little more abundant, longer, and erect at the lateral margin of the first tergite and tufts of appressed, similar pile, some of it shorter, some of it longer, on the lateral margins of the remaining tergites but never comprising massive tufts on the tergites themselves. I find 7 well-developed tergites visible above in the females, but arising from the remaining recessed tergites and sternites, there is below the seventh tergite, a great mass of tangled, dense, pale pile forming an enclosure about the female terminalia: the amount that is exposed varies greatly, sometimes very extensive and again tucked within the terminal recess of the abdomen.

Material available for study: A series of individuals of the type-species collected in southern Brazil.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no record of the behavior of these flies.

Distribution: Neotropical: *Ylaoia pegasus* (Wiedemann), 1928 (as *Anthrax*).

Genus *Doddosia* Edwards

FIGURES 149, 155, 431b, 698, 722, 931, 932

Doddosia Edwards, Eucycl. Ent., Paris, ser. B. II, Dipt., vol. 7, p. 103, 1934. Type of genus: *Doddosia picta* Edwards, 1934, by original designation.

Australian bee flies of medium size which show a somewhat greater resemblance to *Lyophlaeba* Rondani than to *Comptosia* Macquart and which possess the large tuft of long, soft, white pile on the anterior metapleuron in front of the spiracle, a characteristic of the South American group of related genera. The sides of the abdomen are parallel, the costa is slightly widened before the middle. The attenuate third antennal segment is styliform at the apex, the proboscis is more than $1\frac{1}{2}$ times as long as the oral recess. Wings are banded but the brown color is very diffuse; radial loop of only medium length; only 2 submarginal cells

present; anal vein straight, except at apex, the alula short and plane.

Known only from Northern Queensland. The type material came from Townsville; the material I have collected came from near Dimbula, Queensland.

Length: 12 to 14 mm.; wing length 12 to 14 mm.

Head, lateral aspect: The head is hemiglobular; the occiput is comparatively extensive above, strongly sloping inward and twice as long dorsally as below. The pile of the occiput is fine, flat-appressed, sericeous, slightly flattened and reaching the eye margin. The interior collar is quite short and rather scanty. The front is short and, together with the face, does not extend beyond the eye in the lateral aspect. The frontal pile is abundant and coarse and obliquely turned downward and rather more dense in females. The eye is reniform with a quite deep, broad indentation below the middle; the angle above is equal to the angle below. The palpus is composed of a very short, fused basal segment and a much longer, curved, clavate, apical segment, which has a scanty fringe of long, fine hairs below. The proboscis is short and quite stout, the labellum large, flat, and elongate oval with interior rows of small tubercles; proboscis a little longer than the head and at rest extends upward obliquely between the antennae. The antennae are attached at the middle of the head. The first segment is large and swollen, widened inwardly at the apex and bears dense, long hairs below, and shorter setae above at the apex, besides longer hairs dorsolaterally. The second segment is much smaller, beadlike, strongly divergent; the third segment is not as wide as the second but gradually attenuate from the base to the styliform apex. This segment is as long as the first two segments together and bears a minute, apical spine.

Head, anterior aspect: The head is circular, as wide as the thorax. The eyes in the male are holoptic or virtually so for a distance a little greater than the vertical triangle. They are separated at most by half the width of an ocellus. The male front is an equilateral triangle, pollinose, with scanty, long, yellow pile laterally and a bare streak down the middle. Front extended forward as a triangular tongue between the antennae. In the females the eyes are separated by about 3 times the distance between the posterior ocelli. The front in females has similar pile to the male. Ocellar tubercle small, low, long-isosceles. The oragenal recess is deep throughout and is slightly narrowed anteriorly, and it ends a considerable distance from the antennae but the inner foveate recess is widest anteriorly and narrows below. This is because the walls of the oragenal recess are thick and wide but have an odd, curious, oval hollow on each side on the lower half. Tentorial fissure moderately deep, beginning on the lower half of the head, and the whole sides of the face densely obscured by long, extensive pile. The face medially is more extensive and vertically it is nearly but not quite as long as the first antennal segment. The antennae rest upon a placodelike, basal

sclerite. The gena is moderately extensive below the eye, polished, shining, without pile, whereas the pile on the sides of the face is strongly directed downward. The pile on the sloping part of the face, adjacent to the eye margin, and along the middle of the oragenal recess is directed straight outward. Viewed from above the occipital lobes are tightly adjacent. The occipital recess is rather large.

Thorax: The thorax is compact, the mesonotum low and gently convex, faintly pollinose, densely covered with glittering, golden, curled, flat-appressed, slightly flattened pile. The thorax also has a considerable amount of fine, erect, brownish-golden pile which anteriorly becomes quite dense, especially in the male. There is similar, long, brownish-golden pile distributed very densely along the anterior mesonotal margin, on the whole of the humerus, which is much obscured, the whole notopleuron, and shorter but densely on the postalar callosity. The notopleuron has 2 bristles. Scutellum large, triangular, with pile corresponding to the mesonotum. Pleuron everywhere densely pollinose and conspicuously pilose. Whole of the mesopleuron and almost the whole of the sternopleuron with tangled mats of long pile. Only the pteropleuron and hypopleuron lack pile. The lateral metanotum, the anterior metapleuron in front of the haltere especially, and the metapleuron behind the spiracle are all rather densely, long pilose. Squama with a wide, plumose fringe.

Legs: The legs are well developed but with the first 4 femora scarcely thickened basally. All the femora bear flat-appressed yellow scales and a few fine, suberect hairs posteroventrally; the anterior femur has 1 or 2 setae anteriorly, middle femur likewise; the hind femur has 2 or 3 weak anteroventral bristles and a few minute, anterodorsal setae on the outer half. The anterior tibia has 8 fine, oblique, slender bristles anterodorsally, 6 others posterodorsally and 8 equally minute bristles posteroventrally. The middle tibia has 6 slender bristles anterodorsally, 6 others slightly more stout posterodorsally, and with 6 posteroventrally. The hind tibia is long and slender; it bears 12 short, moderately stout anterodorsal bristles, 9 fine, anteroventral bristles, 8 fine, dorsomedial bristles, and 18 fine, oblique, ventromedial bristles. The anterior basitarsi are as long or longer than the remaining segments and with oblique, spiculate setae below. The claws are slender, but wide at the base, sharp at the apex, rectangularly curved at the apex and with long, slender, spatulate pulvilli, and short, triangular arolium.

Wings: The wings are much longer than the abdomen, large, with the anterior border brown extending to the end of the second vein. The brown color extends obliquely across the wing to just beyond the third vein at the origin of its anterior branch and again extends all the way across the wing on the outer half of the discal cell to the end of the third branch of the medius. Also, the whole of the first and most of the second basal cell is brown. The second vein forms a well-developed radial loop extending to the end of the mar-

ginal cell outward and downward. There are only 2 submarginal cells. The first posterior cell and anal cell are widely open. The anterior crossvein enters the discal cell at the outer fifth. Axillary lobe well developed, ambient vein complete, the alula 3 times as long as wide, its posterior margin plane.

Abdomen: The abdomen is elongate, longer than the thorax, and with parallel sides in both sexes. It is feebly shining brownish black with 7 well-developed large tergites in the male and a short eighth tergite recessed under the seventh but a little longer laterally, in addition there appears to be an equally short, hood-like, ninth tergite overhanging the terminalia. Females with 7 well-developed tergites. Any additional ones are completely concealed and the female terminalia densely enclosed and laced about by long, matted, flattened, golden hairs. The pile of the abdomen consists of rather numerous, quite long, erect, golden hairs on the first three tergites, never dense, becoming shorter and fewer posteriorly and with a few very fine, blackish hairs appearing on the last three tergites. In addition, however, there is a conspicuous, posterior border of flat-appressed, curled, golden, flattened pile on the first seven tergites which is somewhat more extensive near the lateral margin, especially more extensive on the fourth tergite and beyond. The male terminalia are exposed ventrally, the basistyle large and adjacent.

The male terminalia from dorsal aspect, epandrium removed, show a figure rather similar to *Comptosia* Macquart. The dististyli are quite large, very blunt, and truncate apically. The epandrium is reduced in size and is narrow. In all of these the epandrium shows a strong basiventral lobe.

Material available for study: A series of males and females of the type-species that were collected by the author near Dimbula, North Queensland, September 1953.

Immature stages: Unknown.

Ecology and behavior of adults: The flies that I have collected were alighting on damp sand in a small, otherwise dry, stream bed.

Distribution: Australian: *Doddosia picta* Edwards, 1934.

Ulosometa, new genus

FIGURES 431C, 929, 930

Type of genus: *Ulosometa falcata*, new species.

Large, relatively bare flies with peculiar wings. They are reddish brown with black mesonotum, its borders reddish. The abdomen is rather flattened, wider than the thorax, and narrowed only beyond the fifth tergite; 8 tergites are visible above in males. The pile is fine, short, yellowish, scanty, and curled like wool, and appressed.

These flies are related to *Ylasoia* Speiser and possibly to *Oncodossia* Edwards, but differ in the wing and wing venation. The apex of the wing is hook-shaped as

in certain nemestrinids and has a somewhat similar pattern. They are sharply maculate with a reddish-brown foreborder and also with an irregular broken series of vertical bands: one subbasal, one beyond the middle, and a third along the apical border to the wing apex. Venation peculiar and erratic. There are 3 submarginal cells; the anterior crossvein lies almost at the end of the long, widened, posteroapically hollowed discal cell; first posterior cell greatly narrowed on the wing margin; third posterior cell also much narrowed on the margin from both directions, leaving it short and club-shaped above and obtruded forward into the end of the discal cell. Anal cell open. Uncolored areas clear except for brownish-yellow villi. In males the eyes are narrowly separated by the thickness of the second antennal segment; first segment large, short, swollen; third segment elongate, slender, tapered, narrow. Male dististyle elongate and protruding to the left.

These flies are known from a single species from Tucuman, Argentina.

Length: 17 mm.; wing 16 mm.

Head, lateral aspect: The head is comparatively short from the lateral aspect. The occiput while prominent is greatly rounded and sloping backward and inward to the rim of the moderately large circular cup. The eye is reniform, indented, but not deeply indented, and without a bisecting line. The upper eye facets in the male are scarcely enlarged. The eye is more than twice as high as long. The face does not protrude forward beyond the eye margin, but the entire face and the upper genae are densely covered with a very coarse, erect, reddish, bristly pile, with similar pile intermixed upon the lower surface of the first antennal segment. The occipital pile is similarly colored but scanty, short, and flat-appressed.

The proboscis is short and stout with a long, robust labellum and extends a little beyond the apex of the oral cavity, to rest between the large, stout, first antennal segment. Palpus composed of 2 segments but of no great length, its pile minute. The front is flattened and depressed down the middle and bears a lateral patch of dense, gray, bristly pile diverging outward along the eye margin. The antennae are attached just above the middle of the head. The first segment is 3 times as long as the second segment and more than twice as wide as the second segment. It bears dense, reddish, bristly pile laterally, medially, and still longer dense, red pile ventrally. The third segment is less wide than the second, tapers rapidly from the base to the apex which has a minute, spine-tipped microsegment. The third segment is very little longer than the first segment.

Head, anterior aspect: The head is much narrower than the thorax and even narrower than the humeral space. The males are dichoptic and eyes separated by nearly the width of the ocellar tubercle. The ocellar triangle is elongate, distinctly raised above the eye margin, and the posterior ocelli are set forward a short

distance from the posterior eye corner, and this tubercle bears a dense patch of reddish, bristly pile curving forward. The antennae are separated by rather more than the thickness of the second antennal segment and has a distinct groove between them. The oragenal opening is elongate and comparatively deep with vertical and hollowed sides and the genae are shelved deeply inward along the conspicuous tentorial fissure. Behind the proboscis the ventral occiput is excavated and striated. Upper genal pile short, erect, bristly becoming longer as it merges with the pile of the face. From above the occipital lobes are adjacent with shallow crease between.

Thorax: The thorax is quadrate, slightly wider across the prominent, swollen, postalar callosity. The humeral callosity is prominent, sharply margined laterally, vertically platelike behind. The pile of the mesonotum is scanty, erect, bristly, and short. There are 2 or 3 distinct, short, black bristles on the notopleuron. Center of mesonotum broadly opaque black with reddish border on all sides and a large, dull, red rectangle in front of the scutellum. The scutellum has a broad, deep, transverse fossa at the base which is broadly rounded below. It is barely notched medially at the apex, the whole surface reddish with median stripe of pale, brownish-yellow or whitish pollen, and a few scattered, appressed, short, bristly hairs, especially on the margin. The pleuron is almost entirely brownish red, dully black in the lower anterior corner of the metapleuron and black above the coxae. There is a small tuft of long hairs in the lower corner of the pteropleuron; the metapleuron is bare, but the metanotum has dense, red pile. There is a tuft of red pile below the haltere which is situated some distance behind the spiracle. The plumula is absent, but there is a curious tuft of rather dense, long, fine pile extended outward from an oval patch on the anterolateral portion of the postalar callosity. Squama with a broad, wide border of long, fine pile.

Legs: Legs are rather small, the tarsi short, especially on the middle and hind pairs, where they are distinctly shorter than the tibia. The femora are shining and without scaliform pile but with scattered, appressed, short, bristly hairs. The tibiae likewise have appressed short, bristly, reddish yellow hairs and also several rows of short, strongly appressed, fine, black bristles, 15 to 20 in each row. The black ventral spicules of the tarsi are sharp, conspicuous, and appressed. Pulvilli prominent; arolium stublike and distinct.

Wings: The wings are elongate, widest just beyond the middle, narrowing toward base and apex; they are sepia brown in color, etched by yellowish veins, and the edges of the mottled pattern are rather sharp. The auxiliary vein and the first vein end close together. The costal border beyond is strongly thickened; marginal cell rounded and slightly protuberant at the apex. There are 3 submarginal cells. The anterior crossvein enters the discal cell almost at the end of that cell;

first posterior cell much narrowed at the wing margin; third posterior cell almost equally narrowed; anal cell widely open. The wing is densely covered with yellowish villi on the hyaline areas. The reddish sepia color covers the anterior border of the wing backward to the anterior border of second basal and discal cells; the wing is more yellowish in the middle, and more brownish obliquely across the base of the second and third basal cells, and the axillary lobe. There is also an irregular, vertical stripe at the end of each of these 3 cells, which extends over narrowly into the base of the discal and fourth posterior cells. There is a more prominent, oblique, crossband covering the outer third of the wing and edging both sides of the third posterior cell, the anterior border of this cell, the whole apex of the discal, also the basal border of the first posterior cell and its anterior border; it continues to the anterior border of the wing, and then borders the anterior branch of the third vein, and the apex of the second vein. Base of the costa with a lobe instead of a hook.

Abdomen: Elongate, oval, a little convex, a little wider than the mesonotum; rather bare but possibly partly denuded; the pile is fine, flat-appressed, and reddish. The whole abdomen is reddish brown with obscure blackish bands basally on the third to fifth tergites becoming narrower and reduced on each succeeding tergite. There are 6 tergites, which are of nearly equal width. These are only slightly reduced progressively in length. The seventh and eighth tergites, while conspicuous, are more narrowed and form a shovellike hood for the terminalia. The male terminalia are terminal, large, conspicuous, toothlike and extended to the left.

The male terminalia from dorsal aspect, epandrium removed, show a body which is long, and somewhat wider than *Bryodemina* Hull. Likewise, it has nearly parallel sides and therefore with very little taper. The base of the aedeagus is large, the lateral apodeme is much larger and triangular. The epiphallus is constricted in the middle and like *Bryodemina* Hull not reaching the end of the basistylus. The basistylus itself is quite long but stout. Epandrium triangular, the basal ventral lobe much thicker.

Material available for study: Two males, the unique type and paratype, from Tucuman, Argentina, May 7, 1918. Species description incorporated in the generic description; type in the National Museum of Natural History.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical: *Ulosometa falcata*, new species, as described above.

Genus *Oncodosia* Edwards

FIGURES 152, 153, 427, 699, 723, 933, 934, 935

Oncodosia Edwards (Encycl. Ent., Paris, ser. B. II, Dipt., vol. 7, p. 101, 1934. Type of genus: *Anthrax patula* Walker, 1849, by original designation.

Large flies rather readily recognized by the pattern of the wing and its pointed apex and relatively broad base. Moreover, the alula is large and extensive, and the anal vein is distinctly bowed backward in the middle. There are normally only 2 submarginal cells, the anal loop is short, but in typical species the discoidal cell is acutely pointed apically. As to the wing pattern there is a brown foreborder ending with the first vein and extending obliquely backward to fill the base of the first posterior cell, whole of first basal cell but only narrowly along the edge of the discal cell; in addition there are 4 isolated spots along the posterior part of the wing.

Characteristically the abdomen quite broad, broader than the thorax, and has dense, rather flattened tufts of long hair along the lateral margins of the tergites in contrast to the short, appressed pile over the remaining dorsal surface. The antenna is short and attenuate but with a very fine stylelike, unsegmented extension at the apex.

These flies are only known from Western Australia. Length: 15 to 18 mm.; of wing 18 to 19 mm.

Head, lateral aspect: The head is hemiglobular with the occiput quite extensive and prominent above but strongly sloping inward. The pile of the occiput consists of very minute, short, erect or subappressed setae in scanty quantities. In addition, the central fringe on the border of the occipital recess is very short and appears to consist of only one or two rows of hairs. There is a curious, impressed collar quite near the ocular margin extending from near the vertex to the lateral indentation of the eye. The front in the male is a little swollen but from the lateral aspect scarcely extends beyond the eye. This is likewise true of the face. Pile of the front is dense, fine, bristly, and erect. Within the middle, between the widely separated antennae, there is a wide, curious patch of flat-appressed, golden pile. The eye is reniform and in spite of the shorter occiput on the lower half of the eye, the eye is shorter on this lower half because of the receding face.

Proboscis slender, a little widened at the base, the labellum flat and oval and somewhat pointed apically. The proboscis is longer than the head and in repose extends up and between the antennae. Palpus small, slender, a little clavate apically and with fine hairs below. The antennae are attached slightly above the middle of the head; the first segment is large, robust, barrel-like, and although truncate apically and slightly oblique, it is not swollen inward at the apex. It bears very dense, bristly pile, especially bristly medially and above but a little longer and quite coarse ventrally. Second segment attached on the outer edge of the first segment, small and beadlike with numerous, short, black setae dorsally and laterally only. Third segment at the base almost as wide as the second segment. It is a little compressed laterally but from the lateral view it is short-conical, and bears a short, apical spine.

Head, anterior aspect: The head is circular, much more narrow than the thorax and relatively small. The

eyes are separated in the male by a distance equal the width of the posterior ocelli from their outer edges. The ocellar tubercle is a little swollen and short isosceles. The posterior ocelli very narrowly separated from the eye. The antennae are unusually widely separated and far apart; they are actually closer to the eye margin than they are to each other, the distance between being almost equal the maximum width of the greatly swollen first segment. The orageal opening is shallow, except below where it is moderately deep; it is also narrowed above and fails to reach the antennae by a distance equal the width of the first antennal segment. This middle part of the face is bare, but on either side there is a large, extensive patch or clump of numerous, long, fine, erect, rather stiff hairs, black ones above and yellow ones below. At the lowest point of the face where it shelves deeply inward to the deep tentorial fissure, there is a dense patch of long, erect pile. The genae are narrow, a little more extensive at the bottom of the eye but much less so than in *Comptosia* Macquart. The eye is pilose and conspicuously pilose on the lower half. There are only a few scattered hairs on the upper third of the eye and these upper facets are scarcely enlarged in the male. The head viewed from above shows the occipital lobe to be very tightly appressed and the depression shallow. The ocellar tubercle extends behind the eye.

Thorax: The thorax is large, the mesonotum quite low, rather strongly flattened on the posterior half and only slightly convex anteriorly. It is much wider posteriorly than anteriorly. It is pollinose with narrow, medial, linear vittae, feebly shining behind and very densely covered with short, suberect, or slightly appressed, coarse, pale pile, which becomes more matted and appressed laterally, but changes along the anterior margin to a dense collar of long, erect, bristly pile, which extends over the broad humerus. Whole lateral margin from humerus to wing also has many reddish bristles mixed with pile. The notopleuron has 5 more stout, slightly longer reddish bristles. Postalar callosity with an extraordinarily long, bushy tuft of dense, fine pile on the sides of the vertical surface behind the wing, with shorter pile in front above and with 8 or 10 red and some black bristles on the dorso-lateral border of the callosity.

The scutellum is quite large tending to be very obtusely triangular and quite rounded apically. At the base, it and the preceding mesonotum are both sharply declivitous with deep, trenchlike furrow. Postmargin of the mesonotum with long, fine, curled pile. Scutellar disc with dense, fine, erect, mostly black, bristly pile. The margin of the scutellum has short reddish and black bristles which are distinctly slender. Squama with a wide band of plumoselike pile. Pleuron quite thinly pollinose, the pteropleuron and hypopleuron bare, the whole of the mesopleuron with dense, long, fine pile and a cluster of slender red bristles dorsally curled upward. Upper sternopleuron with scattered, tangled pile, propleuron and prosternum with much

long, bristly pile. The lateral metanotum is very short dorsally; it bears dense, long pile laterally. The anterior metapleuron is completely without pile in front of the haltere, but there is a conspicuous patch of long, fine pile behind the spiracle. Halteres small and slender.

Legs: The legs are stout, the tibiae are almost as thick as the femora. The first 4 femora are only slightly enlarged toward the base; all 3 pairs of femora are covered densely with fine, flat-appressed, shining, slender, reddish brown, flattened pile. Anterior femur with 3 or 4 fine, anteroventral bristles, and postero-ventrally with some 10 still finer and shorter bristles and some additional fine pile. Middle femur with 10 longer, stouter, anteroventral bristles, but posteriorly and ventrally with only very fine, suberect hairs. Hind femur with 7 or 8 fine, slender oblique, anteroventral bristles, smaller than those on the middle femur and a few small setae ventrally. The anterior tibia is shorter than the middle tibia, the middle tibia shorter than the hind tibia. The hind tibia is as long as its femur and is slightly curved. Anterior tibia with several rows of minute, bristly spicules; there are 12 anterodorsally, 8 posteriorly, 6 or 8 ventrally, and the same number of much smaller ones posterodorsally. Middle tibia with similar bristles in length and number. Hind tibia likewise with the bristles short and slender, the numbers are also about the same as the middle tibia. There are 12 on the ventromedial row; those dorsally are scarcely longer than the numerous, fine, oblique setate hairs. There are at least 12 that stand out as weak bristles. Tarsi rather short, terminal segment slender. Claws slender, strongly bent on the apical half, the pulvilli long and slenderly spatulate. Arolium distinct but short.

Wings: The wings are quite large and long, much longer than the abdomen, very broad at the base with a large, extensive alula. The costa at the base is greatly thickened and expanded and has a conspicuous comb of setae in the male. The costal cell is wide both before and after the humeral crossvein. The wing is rather pointed, the marginal cell widened apically and bulging outward at the apex, although the radial loop is not deep. There are only 2 submarginal cells, the first posterior cell is narrowed at the margin; the anal cell is likewise open and also of about the same width as the first posterior cell. The anal vein is distinctly bowed back in the middle, therefore slightly sinuous. The anterior crossvein is very much oblique, entering the discal cell near the outer fifth. Anterior border of wing reddish brown, the red ending on the foreborder opposite the base of the second submarginal cell, then extending obliquely backward, it extends a little beyond the first basal cell, narrowly borders the discal cell in front and fills out the basal half of the second basal cell, extreme base of the third basal cell, and the whole of the alula. There are prominent brown spots below at the end of the second basal cell, along the discal cell at the furcation of the fifth vein, below at the end of the discal cell, and a round spot at the base of the sec-

and submarginal cell. Remainder of wing hyaline, thinly villose, ambient vein complete.

Abdomen: The abdomen is extremely broad, only a little convex, tending to be flattened especially on the posterior half, short oval. It is much wider than the thorax, shining brownish yellow with a series of small, blackish triangles basally in the middle of the second to the sixth tergite. The first tergite entirely black, except for linear, yellow hind border. This segment bears dense, long, fine, yellow pile extending even under the scutellum, subappressed across the middle, remarkably dense, longer, erect but fine laterally where it looks like cottony tufts. Wide middle portion of the tergites covered with fine, appressed, short, black and partly yellow pile, the black pile denser along the anterior margin of the second tergite and on all of this central area beyond the base of the second tergite the pile is quite sparse. Laterally, however, far out on the edge of the tergites there are very dense, lateral, flattened tufts of conspicuous pile; the pile of the posterior corners pale yellow tending to be more appressed backward and tending to narrowly follow the posterior margins inward on the outer third and the anterior corners with equally conspicuous tufts of black pile which tends to be less strongly turned backward. I find 7 well-developed, visible tergites in the male from

above. There is an eighth completely recessed beneath the seventh and in addition a smaller, apically notched, recessed, ninth tergite forming a hood over the small genitalia. The apices of the two pieces can barely be seen beneath.

The male terminalia from dorsal aspect, epandrium removed, show short, almost triangular dististyli; the base of the aedeagus seems undifferentiated from the epiphallus. The lateral aspect shows a long, rather stout basistylus. The epandrium and the entire structure is very similar to *Doddosia* Edwards. It differs principally in the dististyli and the epiphallus. Like the other members of the Comptosini, the epandrium has a prominent basiventral lobe.

Material available for study: I have a male of *Oncodosia plana* Walker, which I collected in Western Australia, January 6, 1954. According to the figures given by Edwards the wing of *Oncodosia plana* Walker is almost identical with the wing of the type-species, *Oncodosia patula* Walker.

Immature stages: Unknown.

Ecology and behavior of adults: This species can be collected on low-growing flowers of *Leptospermum*.

Distribution: Australian: *Oncodosia ampla* (Walker), 1852 (as *Anthrax*); *patula* (Walker), 1849 (as *Anthrax*); *plana* (Walker), 1849 (as *Anthrax*).

Subfamily Exoprosopinae Becker, 1912

The flies of this very large subfamily fall within some 35 genera and many subgenera centered around the enormous and worldwide genus *Exoprosopa* Macquart with its 443 described species.

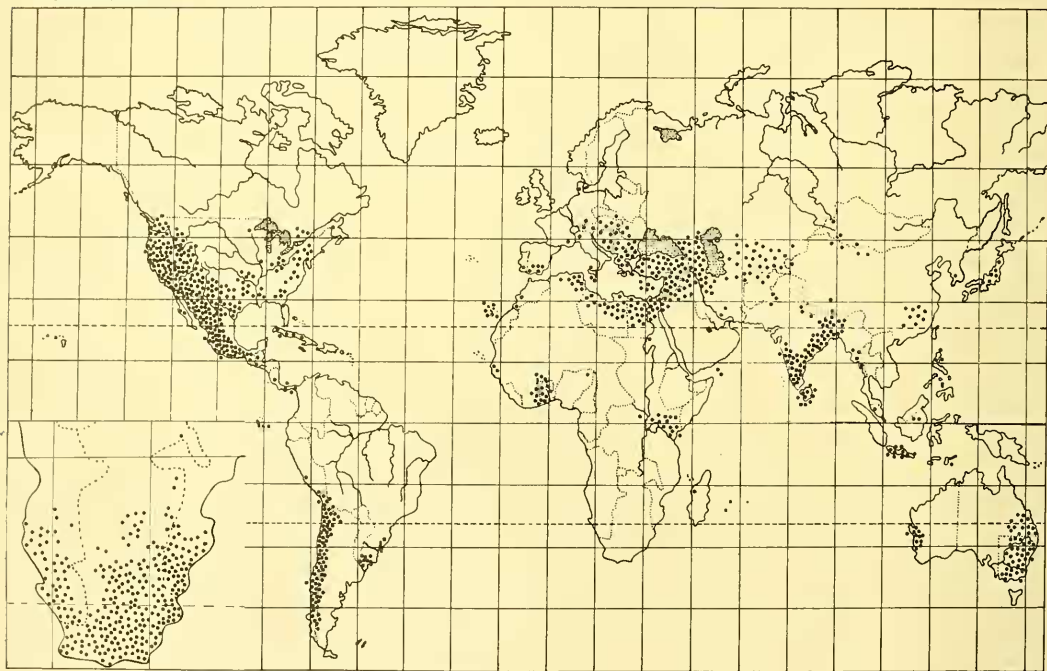
The outstanding characteristics of the subfamily lie within the condition of the posterior eye margin, which is strongly indented but is variable with respect to the presence or absence of a sharp notch or bisecting line. All of these eye characters need to be correlated with genitalic characters as well as the extraordinarily numerous divergences of wing venation. This involves a special morphological study of the genus *Exoprosopa* Macquart in particular, but also of related genera. Dissection of many genera of this subfamily has shown a distinctly unique characteristic of the epiphallus: from the dorsal aspect it is curiously a broad, apically rounded, tongue-like process proceeding from a swollen base.

I recognize 3 tribes: the Exoprosopini, with the majority of species; the Villini, with a very large number of species and like the former group, also worldwide; and the Villoestrini, a small group and a probable offshoot from the *Villa*-like ancestry, which are peculiar for the remarkable and complete loss of effective mouthparts. This is total in *Villoestrus* Paramonov, and virtually so in the other genera that fall here. These are found on 4 continents.

Tribe Exoprosopini

These flies of worldwide distribution are characterized by great diversity and have appropriately been divided into many subgenera. Most species are large and some are veritable giants among the bee flies,

Exoprosopinae



TEXT-FIGURE 45.—Pattern of the approximate world distribution of the species of the subfamily Exoprosopinae.

reaching a wing expanse as in *goliath* Bezzi up to 64 mm., in others with a wing spread of as little as 12 to 14 mm. In this tribe the more distinctive genera are *Isotamia* Bezzi (described under three names), *Litorrhynchus* Macquart, *Ligyra* Newman, and *Colossoptera* Hull. *Diatropomma* Bowden also is unusual. The genus *Exoprosopa* Macquart is one of the most remarkable in the entire family. It is worldwide in distribution, and several hundred species have been described and undoubtedly many more remain unknown. Also, much work remains to be done in the analysis of this one genus, and I believe when all of the terminalia can be completely dissected and delineated and compared, that it will be necessary to recognize additional genera and subgenera. There appears to be immense variety in the patterns of the wing and in all accompanying features.

Villini, new tribe

Bee flies ranging in size from 4 to 5 mm. in length to 16 or 17 mm. Antennae widely separated and the third antennal segment bulbous at base, the style short to long, the thickness variable and the style nonarticulate except rarely. Metanotal and metapleural pile tufts present, often dense. Squamal and alary scales narrow. Oral opening in some forms greatly reduced. Proboscis generally shorter than oral recess and with fleshy labellum but in some genera distinctly longer than head, more slender throughout and at apex. Anterior tibia varying from smooth, without bristles, and reduced in size, to normal in size, and with well-developed slender bristles or smaller spicules. Wings with 2 to 3 submarginal cells. Costal comb usually prominent. Pulvilli generally absent, occasionally present.

It is not easy to find a dependable means of separating the Villini group of genera from the Exoprosopini group of flies. Points of overlap occur in the number of submarginal cells; there are a few species of *Thyridanthrax*, like *ternarius* Bezzi and *laetus* Loew, which have 3 such cells yet are so clearly like *Thyridanthrax* in other respects that there is little doubt of their position. Many of the Villini are very distinctive: such are *Cyananthrax* Painter, *Diplocampta* Roeder, *Lepidanthrax* Osten Sacken. Also *Poecilanthrax* Osten Sacken, *Dipalta* Osten Sacken, and *Hemipenthes* Loew, and *Paravilla* Painter are each rather distinctive.

American species of *Thyridanthrax* Loew show the distinctively triangular face of the type-species, and in Europe this genus often shows a very blunt face and these I assign to *Tauropsis*, new subgenus, with *irrovellus* Klug as type. Also in European species the third antennal segment varies from the typical form with the stylate part abruptly formed and much narrowed and attenuate but far from linear, to those like

misellus Loew and *semifuscus* Engel where it is long, scarcely tapered, and at the tip end thick and stout. Still others have the segment form typical but with a short, yet distinct microsegment as in *Exoprosopa* species, such as *stigmulus* Klug and *afer* Fabricius, which, however, are readily distinguished from *Exoprosopa* species by the untoothed claw and other differences. The variability of the third antennal segment is also well shown in such species as *Exoprosopa subfasciata* Engel, where it is quite long, of uniform thickness, not at all tapered, and lacks an apical style; this species should be assigned to *Corycetta*, new subgenus.

Four characters distinguish these two tribes, and the allocation of an unknown fly to one or the other depends upon the preponderance of characters. For example, in those rare species of *Thyridanthrax* which have 3 submarginal cells (the *ternarius* Bezzi, *laetus* Loew group) claws lack the basal tooth, ocelli are remote, or antennal style is undivided.

Host selections where known are quite diverse. Larvae of: *Rhynchanthrax* Painter parasitize species of *Tiphia*, *Tiphia* parasitizing white grubs; *Paravilla* Painter, bembecid wasps; *Chrysanthrax* Osten Sacken, scoliid wasps in turn preying on white grubs; *Thyridanthrax* Osten Sacken parasitic on tsetse fly puparia, and other muscoid flies, such as *Calliphora*, and living also more commonly in the egg cases of locusts; *Hemipenthes* Loew behaving as hyperparasites attacking species of *Ophion*, *Banchus*, and tachinids such as *Masicera*, which in turn attack nocturnal Lepidoptera; *Villa* Lioy, primarily parasites of nocturnal Lepidoptera, but also tenebrionid beetles in North America and northeastern Europe; *Dipalta* Osten Sacken parasitic on myrmeleonids; *Poecilanthrax* Osten Sacken parasitic on a variety of nocturnal Lepidoptera such as cutworms, sod worms, etc.

There has been much discussion by various authors of the taxonomic limits of *Villa* Lioy, *sensu stricto*. Much of this is due to overlapping in different taxa of characters that must necessarily be used in defining the genera and subgenera of what might be called the *Villa* complex in the wide sense (and for which I here erect the tribe Villini). In this tribe there are some 10 to 15 genera, of which 6 are of particular interest: *Villa* Lioy, *Hemipenthes* Loew, *Thyridanthrax* Osten Sacken, *Chrysanthrax* Osten Sacken, *Paravilla* Painter, and *Rhynchanthrax* Painter. Painter (1965) places all of these as subgenera of *Villa* Lioy. Engel treated *Thyridanthrax* Osten Sacken and *Hemipenthes* Loew as entirely separate genera, treating 48 Palaearctic species of the former genus and 10 species of the latter. Bezzi (1924) in his Bombyliidae of Ethiopia took the same view and so has Hesse (1956) in his monumental study of South African bee flies. Still more recently Bowden (1964) segregated these forms away from *Villa* Lioy; in spite of what appears to be overlapping, I believe Bowden's is the correct view.

While admitting the relatively close relationship of these several taxa, my own studies lead me to believe

that systematic and bionomic studies are better served by leaving them as separate genera until such time as a complete study of the genitalia of all or nearly all species can be made. This provision reduces the use of trinomials. Certainly there is no doubt in my mind that the very interesting taxon *Rhynchanthrax* Painter is distinctive, separated by the characters discussed under that genus. And I feel that the same can be said of *Paravilla* Painter with its conical face. Probably facial contours, length of antennal style, and length of proboscis on the whole provide more valid relationships than wing patterns, which, to some extent, may tend to repeat themselves in certain genera. To assist in clarifying the above genera I have illustrated the faces, wings, and antennae of typical species of each.

Villoestriini, new tribe

In this group I place four remarkable genera, all of which show profound reduction of the mouthparts. These flies seem to be nearest related to the genus *Villa* Lioy and a probable offshoot from this ancestral line. The male terminalia suggest *Villa*, and Hesse (1956)

finds a resemblance to the *leucochila* species group of *Villa*. These flies are widespread, ranging from South Africa, where three of the four genera are found, to Palestine and to the southwestern United States and Brazil. Besides the reduced mouthparts they are notable for the small antenna, the blunt, short, rounded, and retreating face, absence of pulvilli, large costal comb, etc. The hosts for one species proves to be cossid larvae.

The hypopygium in the Exoprosopinae is rather readily characterized by the extraordinarily long, quite wide, tongue-like epiphallus. Nearly all of the genera have the hypopygium wider on the basal half, distinctly narrowed apically, usually the whole apical half dominated by the conspicuous epiphallus. This will be especially noted in genera like *Oestranthrax* Bezzi, *Astrophanes* Osten Sacken, *Dipalta* Osten Sacken, and many others. Also the dististylus is characteristically subapical in position, almost always small, with a distinct dorsoapical incision and upturned hook. This is less conspicuous in *Astrophanes* Osten Sacken and a few other genera. Such genera as *Chrysanthrax* Osten Sacken, *Hemipenthes* Loew, and *Lepidanthrax* Osten Sacken have a large, wide, rather deep, rounded, anteroventral incision on the epandrium.

KEY TO THE GENERA AND SUBGENERA OF THE EXOPROSOPINAE

1. Mouthparts greatly reduced and vestigial and sometimes entirely absent (Tribe Villoestriini) 2
Mouthparts normal and functional 4
2. Mouthparts completely absent, the oral opening reduced to a minute punctate slit, and even the palpus wanting; pile of face setate. Occiput reduced near vertex.

Villoestrus Paramonov

Minute vestiges of the proboscis remain and sometimes traces of the palpus as well 3

3. Head reduced in size, narrower than the mesonotum at the level of the wings. Third posterior cell relatively short, its base only a little way before the middle vein separating it from the fourth posterior cell, and usually with a short stump of vein projecting into the discal cell from this base. Second vein strongly recurved apically and with a trace of a stump vein basally. Third antennal segment with swollen base, small, short, onion-shaped, the apical piece long and narrow. Occiput quite prominent and tumid near vertex *Oestranthrax* Bezzi
- Head as wide or wider than the mesonotum at level of wing. Third posterior cell relatively long, its base near the apex of the second basal cell and usually without a stump vein into the discal cell. Second vein not strongly recurved apically and without a stump. Third antennal segment more conically stout, the base not strongly constricted, the apical piece not long and narrow.

Marleytimyia Hesse

4. Second vein arising abruptly at a right angle from main stem vein and arising a long distance basal or proximal to the anterior crossvein and arising obtusely rounded anterobasally. Squama fringed with hairs, no scales present. Wings entirely or almost entirely hyaline. (Tribe Xeramoebini) LOMATINAE

The second vein arises quite rectangularly from the stem vein, but usually arises exactly at, or barely before, or barely beyond the anterior crossvein, with which it often appears confluent; distance out of alignment seldom more

than the vein's thickness; sometimes as much as the length of vertical part of second vein. Origin of second vein either rounded anterobasally or with a backward stump vein. In about three-fourths of all species the wings bear characteristic, distinctive patterns of spots and bands, with at least the basal part of wing brown . . . 5

5. Third antennal segment with a small, short, suture-separated microsegment always bearing a tuft, usually a conspicuous tuft, or circle of apical hairs. Face always strongly retreating and rounded below. Oragenal cup short, its walls thin. Gena with a wide, deep tentorial pit or pocket on each side of the reduced upper part of oragenal cup. Proboscis always short and of no great length or size. Metapleuron without pile. Squamal fringe composed of hairs. Claws without basal teeth.

ANTHRACINAE

Attenuate part of third antennal segment with or without suture separated, spine-tipped style, but never with a pencil or circle of hairs at the apex of style or microsegment. Many genera and species fall into each division. The metapleuron is pilose and the fringe of the squama is composed of scales, narrow or wide. Claws with or without a basal tooth. Two, 3, or sometimes 4 submarginal cells present. Oragenal cup comparatively long and narrow, the proboscis enclosed with its recess except when projecting beyond the face; proboscis often much longer than the oragenal cup. No deep tentorial pocket present above the genae. (Exoprosopinae) 6

6. Third antennal segment with a distinctly separated spine-tipped or bristle-tipped style or microsegment, or variable length and thickness, which is separated by a suture, distinct from the base of the third segment. Claws with a basal tooth, long, or short. Three or sometimes 4 submarginal cells present. Ocellar tubercle far from vertex. If a separated style is present together with only 2 submarginal cells, the claws lack teeth; seen in couplet 5B. (Tribe Exoprosopini) 27

- Third antennal segment without any sort of a separated style whatever; it bears only a short spine of variable thickness present at stylate apex. Two submarginal cells or 3 with great rarity. Claws without a basal tooth, a small obtuse tubercle rarely present. Ocelli placed near the vertex. Proboscis long or short. (Tribe Villini) . . . 7
7. Anal cell closed, in or before the margin of the wing. Eye of male separated by less than the width of the ocellar tubercle. Swollen base of third antennal segment very short and wide and saddle-shaped, apical part slender. Face and occiput with broad scales; apex of abdomen broadly silvery scaled . . . *Astrophanes Osten Sacken*
Anal cell open. Eyes of male separated by much more than width of the ocellar tubercle 8
8. Alula absent; axillary lobe also greatly narrowed and reduced. Anal cell widely open. Large flies with very large, long, entirely dark blue wings that are disproportionate to the body. Discal cell narrow, acute apically, with spur vein below. These flies are dark, shining blue, black pilose, the anterior mesonotal pile orange. Face strongly conical, abdomen elongate oval, quite bristly on the sides and scales absent *Cyananthrax Painter*
Flies with the alula present or if narrowed or reduced they are bee flies entirely different in appearance 9
9. Three submarginal cells present 10
Two submarginal cells present 15
10. Wings and other features of face, claws, and antennae as in *Thyridanthrax* Osten Sacken, but regularly with 3 submarginal cells; group *ternarius* Bezzi, *lactus* Loew, etc.
Thyridanthrax Osten Sacken
Wings venation and antenna quite different from *Thyridanthrax* 11
11. Second vein very strongly sigmoid on its outer section, both basally and apically 12
Second vein narrowly curved and marginal cell slightly or moderately bulbous at the apex 13
12. Wing narrowed at base somewhat as in *Mancia* Coquillett, but alula and axillary lobe well developed, but both curves of the last section of third vein broadly rounded. Third antennal segment very strongly onion-shaped at base and the style rising abruptly . . *Diplocampta Schiner*
Wing not conspicuously narrowed at base. Both curves of last section of the second vein rectangular, the base of third submarginal cell with a stump vein above a rectangular supernumerary crossvein. Face bluntly conical, with flattened hairs *Dipalta Osten Sacken*
13. The third antennal segment is conical at base and gently tapered into the antennal style. Face with scales . . 14
Base of third antennal segment small, short, onion-shaped, the style quite long and thin, of uniform thickness. Face with dense, coarse hairs among which are a few flattened hairs. Abdomen with coarse, dense hairs along the sides and a few flattened hairs and with flattened hairs along the posterior margins of the posterior tergites. Basal half of wing generally dark sepia, the apex with one or more spots *Stonyx Osten Sacken*
14. Face bluntly rounded, with short, erect hairs and scalfiform hairs. Upper angle of third posterior cell with a long stump vein into the discal cell. Abdomen with scalfiform pile. Anterior tibia quite without spicules. Wings hyaline.
Atrichochira Hesse
Face conical and with glittering scales. Upper angle of third posterior cell without stump vein. Abdomen with patches of silvery scales along the sides of the tergites. Anterior tibia with weak spicules or setae. Wing black with hyaline base. Discal cell relatively long.
Pseudopenthes Roberts
15. Face very strongly conical and pointed apically and covered with sparse, short, scattered setae. Anterior branch of third vein strongly bent backward and approximately at a right angle. Base of third antennal segment gently tapered and conical. If wing very large and abdomen unusually elongate, the subgenus *Agitonilla* Hull.
Neodiplocampta Curran
Face rounded or conical. Curve of anterior branch of third vein rather shallow, at least not rectangularly rounded. Third antennal segment of various shapes 16
16. Abdomen, especially at the base and sides, and to a lesser extent on the dorsum with matted, broad, conspicuous scales which are often silvery. Proboscis projects well beyond the oral opening. Third antennal segment small, short, onion-shaped, the style long and slender. Contact of discal cell and fourth posterior cell as long or longer than base of fourth posterior cell.
Lepidanthrax Osten Sacken
Abdominal scales narrow, if present at all, and rarely silvery. Proboscis and antenna variable in form and length. Contact of discal cell and fourth posterior cell usually shorter than base of fourth posterior cell . . 17
17. Third segment of antenna short, small, onion-shaped, with long abruptly formed styliform portion which is linear, of uniform thickness, even threadlike. Face and proboscis, each long or short 18
Third antennal segment long or short conical, attenuate beyond the wide base; also rarely, long and thick and scarcely tapered. Face and proboscis likewise variable, long or short 21
18. Alula much reduced, almost wanting; axillary lobe very narrow. Face conical but blunt at apex. The proboscis extends a short distance beyond the oral cavity. Quite small, dark brown or black flies with hyaline wings and brownish yellow, and white or silvery scales on face, frons, thorax, and abdomen *Mancia Coquillett*
Not such flies 19
19. Face produced, bluntly rounded or short conical and the proboscis distinctly extended well beyond the oral opening. Abdomen, especially at the base and sides and to a lesser extent upon the dorsum, is covered with matted, broad, conspicuous scales which are often silvery. Style of antenna long and slender. Contact of discal and fourth posterior cell as long or longer than base of fourth posterior cell *Lepidanthrax Osten Sacken*
Abdominal scales narrow, if present at all, rarely silvery. Face and proboscis of varying form. Contact of discal and fourth posterior cells usually shorter than base of fourth posterior cell 20
20. The proboscis extends beyond the face and oral opening by at least half the length of the oral opening. Styliform part of third antennal segment long and slender. Hypopleuron bare or nearly so. Wing generally with the basal half dark *Rhynchanthrax Painter*
Proboscis not projecting beyond oral opening. Face retreating and generally bluntly rounded. Hypopleural pile usually present. Front tibia generally spiculate. Base of wings blackish on the basal half or more with irregular margin to the black pattern posteriorly. Discal cell at the apex typically expanded, above and below, bulblike and obtuse. Color and wing pattern generally suggestive of *Anthrax* Scopoli species. Pulvilli sometimes present; metapleural fringe scanty and basal comb small.
Hemipenthes Loew
21. Wings hyaline, or very nearly so. Face rounded and retreating and the quite short proboscis does not project beyond the oral opening. Third antennal segment conical but very short, the style long and slender. The pulvilli are absent, the metapleural fringe dense, the basal comb large and often conspicuously silvery. Discal cell acute at apex. Anterior tibia with setae or even spines.
Villa Lioy
Wings partly or wholly colored, or if nearly hyaline the face is either prominent, or the third antennal segment is long conical. Face always more or less extended, bluntly rounded or conical or even sharply conical 22

22. Front tibia spiculate in 3 rows. Face strongly projecting and conical, usually acutely conical. Third antennal segment long conical. *Paravilla* Painter
Front tibia relatively smooth. Claws small, rarely large. Face rounded anteriorly. Face bluntly triangular, or if subconical the wings are large and long. 23
23. Front with rather dense, erect, coarse, bristly hairs; face subconical, with similar hairs but more sparse. Both face and front usually without any appressed, flattened hairs. Wings usually with extensive, mottled pattern covering whole wing, with some hyaline spots; a few species with posterior margin and immediate apex hyaline. Wings unusually large and elongate; first posterior cell characteristically narrowed toward the margin. Lower vein of discal cell bowed, with an angle, and usually with a long, characteristic, ventroapical spur vein or an antero-basal spur vein. End of discal cell acute. Anterior tibia smooth; anterior claws minute. Pulvilli absent.
- Pocilanthrax* Osten Sacken**
At least the apical half or two-thirds of wing clear. Wings relatively much smaller. Pattern of wing on basal half more or less solid and uniform, or with one to several subhyaline flecks, or dilutely hyaline with only the veins and costa of basal half blackish or brownish, or yellow. Discal cell below without angle and lower spur vein. 24
24. Face bluntly but distinctly triangular (sensu stricto), or shorter, subvertical, bluntly rounded (subgenus *Tauropis*, type *irreocellus* Klug). Wings dark at base, but with windowlike hyaline spots about the crossveins and furcations of veins (*fuscistratus* Fallen group). Wings sometimes entirely hyaline (as in *loydii* Austen group), or with the base only narrowly brownish (*aefer* Fabricius group). Third posterior cell varying from very short to very long. Third antennal segment usually short and distinctly conical. Pulvilli absent; front tibia smooth.
- Thyridanthrax* Osten Sacken**
Face more prominent, triangular but never acutely conical, the apex more or less rounded. Style of antenna much more slender near the base of the third segment not at all conical and not onion-shaped either. 25
25. Face prominently protrusive, triangularly projecting and bluntly rounded at the apex. Anterior tibia smooth; pulvilli long and well developed. The second vein arises well before the anterior crossvein. Discal cell at apex wide and truncate. Veins merely tinged with brown at the base.
- Synthesia* Bezzi**
Second vein arising at anterior crossvein or beyond. Inter-calary vein at apex of discal cell much shorter and discal cell not rectangularly truncate. Pulvilli absent. 26
26. Face triangularly projecting but rounded and blunt. Wings dark at base or more or less hyaline, but always darker about the veins, if any color is present. Third antennal segment usually long conical and stylate part quite slender. Contact of discal cell and fourth posterior cell rather generally punctiform or nearly so. Discal cell rather pointed apically. Second posterior cell large. Proboscis confined to oval cavity but, together with labellum, quite slender. Anterior tibiae smooth.
- Chrysanthrax* Osten Sacken**
Face conically projecting, but not acutely pointed. Wings very broad, bluish purple. On the basal half, clear hyaline beyond. Anterior tibiae with microsetae. Proboscis short, stout, the labellum quite short and muscoidlike. Third antennal segment short conical. Second posterior cell much reduced. Discal cell as in *Hemipenthes* Loew.
- Deusopora* Hull**
Wings with 2 submarginal cells. Claws without basal tooth (*lactus* Loew, *aefer* Fabricius group of *Thyridanthrax*).
- Thyridanthrax* Osten Sacken**
Wing with 3 or more submarginal cells. 28
28. Wing with 3 submarginal cells. 29
- Wing with 4 submarginal cells. *Ligyra* Newman
29. Wing partly hyaline and much narrowed toward the base, with both alula and axillary lobe greatly narrowed; thorax short; pleuron relatively bare. Genal grooves indistinct. Proboscis much longer than in *Exoprosopa* Macquart and extending beyond the prominent face by at least the length of the head. 30
- Wing of normal shape, or if rarely narrowed basally the alula is distinct or the proboscis is much shorter. 31
30. The second vein arising distal to the anterior crossvein. Eyes distinctly pubescent under low power. Third antennal segment stout and elongate, with a curious, short-conical cap, and sclerotic apex. *Diatropomina* Bowden
Aberrant flies with the origin of the second vein basal to the anterior crossvein by at least double the length of the crossvein. Wings much narrowed toward the base, alula and axillary lobe both quite narrow and wing blackish on anterior half with irregular margin behind. Proboscis extending beyond apex of the face at least a distance equal the length of the head, and distinctly longer than in *Exoprosopa* Macquart, but the palpi are shorter. The buccal cavity is relatively longer, the pleuron more bare, the thorax shorter, the front claws very short, but front claws less reduced. Postvertex with a very deep transverse furrow. Third antennal segment more like *Anthrax* with almost onion-shaped third segment and with the thin, separated style almost twice as long as third segment. Pulvilli absent. *Isotania* Bezzi
31. Wing entirely iridescent hyaline; at most with very slight, indistinct basal infuscation. Dense, brilliantly shining scales present on several parts of body; hairs pectinate to the base (Bowden, 1964); eyes of male almost touching behind the ocelli. Dististyli deeply U-shaped and curved up at apex. Small species. Bristles on body and legs reduced; integument shining. *Micomitra* Bowden
Wings always infuscated even if only costal cell and parts of basal cells; usually with extensive patterns of brown, yellow, red or blackish, and otherwise differing. 32
32. Large flies with extraordinarily large, long wings, at most feebly shining, more so disproportionate to the body, narrowed basally, much like either *Pocilanthrax* Osten Sacken or *Cyananthrax* Painter, and completely, uniformly, dark sepia in color. Abdomen rather narrowed and doubly as elongate in proportion to *Exoprosopa* Macquart. Second posterior cell more than twice as wide basally as distally; third posterior cell in reverse correspondingly widened on the margin. Tooth of claw long.
- Colossoptera* Hull**
Flies with wing and abdomen normally shaped; venation like *Exoprosopa*, sensu lato. 33
33. Face rounded and retreating. Anterior tibia beset with spicules. Proboscis longer than oral cavity and projecting. Wing venation and pattern characteristic and peculiar. *Littorhynchus* Macquart
Face more or less projecting and generally quite conical. Anterior tibia generally smooth. 34
34. Marginal cell divided into two parts by an anterior, supernumerary crossvein. Wing with numerous, isolated, eye-like spots becoming confluent basally. Small flies.
- Heteralonia* Rondani**
Marginal cell undivided, the wing with only 4 apical cells including the marginal cell. Wings without eyelike spots. 35
35. First posterior cell divided into two parts by a supernumerary crossvein. 36
- First posterior cell simple, open, or closed. 37
36. Second and third posterior cells of unique shape, each long, reclinate, and encroaching upon each other.
- Exoprosopa* (*Exopata*) Coquillett**
Second and third posterior cells of normal shape, very little wider at base than on wing margin, not elongate and encroaching upon each other.
- Exoprosopa* (*Zygodiola*) Bezzi**

37. Discal cell on lower margin, before the tip, with a very prominent angle, emitting an appendix. Terminal vein of discal cell more or less sinuous and running at an angle or perpendicularly to longitudinal axis of wing . . . 38
Discal cell without apical projecting angle below, and if sometimes dilated, it is rounded, not angular, and always without appendix . . . 41
38. Five posterior cells present . . . 39
Only 4 posterior cells present . . . 40
39. Among posterior cells, the third alone closed and provided with a long stalk . . . *Exoprosopa (Mesoclis) Bezzi*
Among posterior cells, the fourth alone closed and provided with a short stalk . . . *Exoprosopa (Metapenta) Bezzi*
40. Front tibia short and thick, beset with well-developed spicules. First posterior cell always open.
Exoprosopa (Acrodisca) Bezzi
Front tibia long and smooth and thin. First posterior cell often closed and stalked.
Exoprosopa (Cladodisca) Bezzi
41. Vein between discal and second posterior cells long, deeply and regularly S-shaped, and in the same line with longitudinal axis of wing, or nearly so. Wings never reduced in size. Discal cell narrow and long, not expanded above or below near its apex . . . 42

- Vein between discal and second posterior cells short, straight or only slightly sinuous; if deeply sinuous, then the vein is short, not S-shaped, or forming an angle with long axis of the wing. Wing sometimes reduced in size. Discal cell shorter, and broader, and sometimes expanded above or below the apex . . . 43
42. First posterior cell closed and ending bluntly, and provided with a long stalk. Hind tibia with very short spicules. Wings with basal half yellow and margined with brown.
Exoprosopa (Trinaria) Mulsant
First posterior cell usually open, or if closed, terminating in a narrow apex and with a short stalk. Hind tibia with long, stout spicules. Basal half of wing not yellow, not margined with brown . . . *Exoprosopa (Defilippia) Lioy*
43. Legs feathered. Discal cell contracted in the middle. Upper branch of third vein not widely divergent from main stem. Marginal cell very narrow at the end.
Exoprosopa (Pterobates) Bezzi
Legs not feathered and venation different. Marginal cross-vein straight or sinuous and recurrent. Second vein originating opposite or before or beyond middle crossvein. First posterior cell typically open, but sometimes closed. Wings never fenestrate, or if so the spots not hyaline. Abdomen with or without silvery bands (including *Argyropsila* of Bezzi, 1924) . . . *Exoprosopa Macquart*

Genus *Villa* Lioy

FIGURES 181, 182, 390, 667, 681, 953, 954

- Villa* Lioy, Atti Inst. Veneto, ser. 3, vol. 9, p. 732, 1864. Type of genus: *Anthrax abaddon* Fabricius, 1794, as *Anthrax concinnus* Meigen, 1820. Designated by Coquillett, p. 619, 1910, the second of 7 (as 8) species.
- Hyalanthrax* Osten Sacken, Biologia Centrali-Americana, Dipt., vol. 1, p. 134, 1887. Type of genus: *Anthrax faustina* Osten Sacken, 1887. Designated by Coquillett, p. 553, 1910, the first of 5 species.
- Aspiloptera* Künckel, Bull. Sci. France et Belgique, vol. 39, p. 145, nota, 1905. Type of genus: *Anthrax flavus* Meigen, 1820. See Bezzi, p. 6, 1924.
- Coquillett (1887), pp. 160-163, key to 52 species (as *Anthrax*).
Coquillett (1887), pp. 170-177, key to 78 species (as *Anthrax*).
Coquillett (1894a), pp. 97-98, key to 16 species (as *Anthrax*).
Becker (1913), pp. 17-67, treatment of Palaearctic species.
White in Hardy (1924), pp. 74-76, key to 13 species.
Bezzi (1924), pp. 182-183, key to 15 species.
Séguy (1926), pp. 192-193, key to 35 species from France.
Painter (1926b), pp. 206-208, key to 9 *Villa* (s. str.) species and 7 related species.
Engel (1936), pp. 571-576, key to 35 males and 32 females of species.
Austen (1937), p. 133, key to 7 species from Palestine.
Hesse (1956b), pp. 472-480, key to 24 males and 24 females species and subspecies.

Small to rather large flies widely variable in many respects but characterized in the following terms: the head is globular, the face varying from entirely rounded and retreating below the antennae to others in which it is very slightly projecting and not quite vertical. The proboscis is always short, not, or at most very slightly, extending beyond the rather ventrally located oragenal recess. The face itself is extensive in dorsoventral length. The widely separated antennae have the third antennal segment with bulblike base but the abruptness

which the style is formed varies considerably. The long, stylate apical part of the third segment is nonarticulate. With rare exceptions most genera in the tribe Villini can in this way be separated from the tribe Exoprosopini. The anterior tibia varies from completely smooth to species that have one or more rows of distinct, fine, sharp, appressed, small spinules.

The type-species of *Villa* Lioy has clear, hyaline wings, except for a varying amount of pale yellow or brownish infuscation at the base and narrowly along the anterior margin; all species, except as noted below, have clear wings with the brown color extending only into costal and marginal cell. In a few species—*fulviana* Say, *occulta* Wiedemann, and a few others—the infuscation, which may be dark, extends diffusely into the cells immediately behind the subcostal; Austen has described a Palaestine species that has *Thyridanthrax*-like pale pattern on the basal third of the wing. Even in those species in which the costal cell is water clear, the subcostal cell is yellow as far as the end of the subcostal vein. Hesse (1956) notes that 2 South African species—*leucophila* Bezzi, etc.—have distinct *Anthrax*-like wing infuscations, but have nevertheless been referred to *Villa*. Hesse further notes that Painter (1930, 1933) in his study of some American representatives of these two genera has relegated *Hemipenthes* as a subgenus of *Villa*. Representatives of *Thyridanthrax* and *Oestranthrax* on the other hand, however, show certain distinct characters that distinguish them respectively and generically from species of *Villa*.

Males of some species have a brilliant mat of silvery patagial scales.

The genus *Villa* Lioy in the strict sense is found on all the continents.

Length: 5 to 17 mm.

Head, lateral aspect: The head is nearly globular, the occiput well developed and long both above and below, but slightly longer dorsally and strongly rounded and sloping backward on all sides toward the large, central, occipital cup. The indentation at the midpoint of the eye margin is shallow but distinct, angulate, and equally extensive above and below the linear division of the upper eye facets. The pile of the occiput is appressed, scaliform, abundant, reaching almost to the eye margin and the interior fringe about the margin of the occipital cup is short and dense. The eye is quite large, sometimes with green reflections, hemicircular in front. The oral cavity and gena are not or only very slightly extended below the eye margin. The extensive frontal area is quite low, convex, and rounded, following the eye margin. Its pile generally is comparatively dense, fine, and erect, varying somewhat in length but usually shorter than the first antennal segment. In addition to the erect pile there is often a considerable amount of flat-appressed scales or scaliform pile, usually of contrasting color.

The face in lateral aspect is short in most species but it varies from nearly vertical on the one hand, to either slightly and bluntly produced, to still other species that are quite rounded, convex, and receding. The pile of the face predominantly consists of suberect, dense, long scales mixed with a certain amount of stiff more or less appressed hairs. The palpus is long and slender, with one segment a little flattened, pointed at the apex, and bears a few fine hairs. The proboscis is always short, usually contained within the oral recess, sometimes slightly protruding beyond. In some species the proboscis seems to be distinctly shorter than the oragenal recess. The antennae are placed at the middle of the head and are relatively small, the first segment is a little widened apically, sometimes nearly twice as long as wide and at least twice as long as the short second segment. The first segment has a tuft of long, stiff, bristly hairs dorsolaterally, a still longer tuft medially, but only a few fine, short setae dorsally. This segment is bare in the middle below and some of the medial hairs may be scalelike. The third segment is bulblike at the base, generally a little wider than the second segment, and apically it bears a stylelike extension, which is not only long but may be formed either abruptly, the quite narrow style rising abruptly from the basal part of the segment, or the swollen basal part may be somewhat conical and only gradually attenuate; generally plane on the dorsal margin but curved and concave below; apex with minute spine.

Head, anterior aspect: The head is as wide as the thorax, sometimes a little wider. The eyes of the male are always separated by approximately the width of the small, raised, ocellar tubercle, which almost touches the eye laterally. This ocellar tubercle varies distinctly in height in species; in some the sides may be quite vertical. In females the eyes are separated by 3 or more times the width of the ocellar tubercle. The ocellar tubercle is small, the ocelli lying either in an equilateral

or a short isosceles triangle and they are placed very close to the posterior eye corners, which are a little rounded. The antennae are widely separated by a distance nearly equal to twice the first segment. The oragenal recess is narrow but quite deep in front as well as behind; it varies in length and is generally wedge-shaped with the sides vertical and plane, but it may be slightly constricted in the middle. The gena consists of a narrow rim at the bottom of the eye and the oragenal recess is sunk below and within the eye margin on the lower half. Viewed from above the occipital lobes are tightly apposed without anterior pit.

Thorax: The general coloration of the thorax is black. The thorax is short, rather flattened especially posteriorly but low throughout and only slightly convex anteriorly. The pile consists of comparatively dense, coarse or fine, erect pile so dense in some species as to obscure the ground color, always dense anteriorly in the region of the collar and along the lateral margins, notopleuron, and above the wing, but often thinning out considerably over the middle of the dorsum, which generally bears a number of flat-appressed, or sometimes loosely suberect, small scales varying from gold to black in color. The notopleuron and postalar callosity at most have very poorly developed, slender, bristly hairs. The scutellum varies in length but is distinctly triangular, its color, pile, and scales corresponding to that of the mesonotum. The plumula is well developed; squama with a long fringe of fine hairs in a narrow plane. The pleuron is densely covered with masses of long, fine, tufted pile, except upon the hypopleuron.

Legs: The femora and tibiae are slender. The femora and especially the hind tibia bear numerous, flat-appressed scales. Anterior and middle femora with a fringe of fine hairs ventrally and posteroventrally, the middle femur often with a distinct row of bristles; hind femur always with a few spines or bristles and often with many. The anterior tibia either with or without bristles or spines; middle and hind tibiae with 4 rows. All the claws are small especially the anterior ones and there are no basal teeth present on claws; pulvilli absent, in contrast to *Anthrax* Scopoli.

Wings: The wings are large, broad at base, pointed apically and are hyaline, glasslike, with wrinkled membrane and slightly iridescent reflections. Quite rarely, as in *Villa fulviana* Say, a faint brown tint from villi is perceptible over the whole of the wing and the costal cell, subcostal cell, and with base of wing in front of alula dark brown; also with diffuse, pale brown color filling out most of the first basal cell and diffusely margining the first vein posteriorly and the anterior crossvein. In *Villa decipula* Austen there is a *Thyridanthrax*-like pattern on the wing, but the face is rounded, the front tibia spinose. Most species of *Villa* Lioy have the costal cell hyaline with only the subcostal cell yellow, but in many species both the costal cell and the subcostal cell are pale yellow, the remainder of the wing hyaline. There are only 2 submarginal cells, but the anterior branch of the third vein, in those species

where it rises plane and nearly rectangularly, sometimes has a short basal spur. In other species this vein is broadly rounded at the first bend. The second vein rectangular exactly at or slightly before the anterior crossvein. The marginal cell is a little widened before the apex. The anterior branch of the third vein has a sharp upward bend near the middle, the vein ending well before the apex of the wing.

The anterior crossvein enters the discal cell at the middle or sometimes a little before the middle. The discal cell is acute and pointed apically in contrast to *Hemipenthes* Loew where it is usually swollen apically and obtuse, and this cell is strongly constricted before the middle. The axillary lobe is large and wide, the alula large but about twice as long as wide, its margin bearing scales. The costa at the base is very greatly expanded with strong, bristly comb, its width about twice that of *Hemipenthes* Loew. Also, the costal hook is spinelike, and the patagium in some species is quite large and conspicuous forming a flat, radiating fan of considerable proportions. In other species it is small and inconspicuous. In those species where it is enlarged it will be yellowish or whitish in the females but brilliantly silvered in the males and this silver pile sometimes extends onto the base of the costa.

Abdomen: The abdomen is relatively short, broadly oval, wide even at the end of the sixth tergite and the whole abdomen wider than the thorax, sometimes of equal width. The abdomen is only gently convex, the pile varying in different groups in the genus. The erect, long pile may be quite dense as in forms like *Villa pretiosa* Loew or *Villa fulviana* Say with, however, one or sometimes two types of flat-appressed pile lying on the tergites. Most species show transverse bands of appressed scaliform hairs or scales on the anterior margins of the second and remaining tergites. These bands are of varying width and color and sometimes narrowly interrupted in the middle. Some species have in addition a rather dense coating of flat-appressed black scales or scaliform hairs over the remainder of the tergites. Lateral margins of the segments either only with appressed, scaliform hair or in the species of longer pile with a very dense lateral border of long, plushlike pile. In some species the pile of the abdomen is not distributed in bands. Sternites largely bare in some species, in others with a dense, matted coat of appressed, scaliform pile. Males of some species have often a dense, shelflike, projecting mat of brilliant silver scales extending out from the posterior margin of the last tergite. Seventh tergite in males of some species sometimes forms a recessed collar around the genitalia. In the more woolly species there are 7 tergites visible from above in both sexes. Female terminalia have a row of small spines on each side.

Because of the large number of species that Dr. A. J. Hesse was able to study and summarize, I quote his work on the hypopygium of the males:

Hypopygium of males markedly uniform in series of species; dorso-apical parts of clasper-like basal parts always covered

with fairly dense hairs; beaked apical joints very uniform in shape and not of much use in the separation of the species, more or less laterally compressed in apical parts and directed slightly outwards, ending apically in an upper tooth-like process or lobe and a shorter lower one; aedeagal apparatus consisting of a slightly curved and pointed aedeagus and a prominent and conspicuous, apically directed, ventral, aedeagal process which is usually in form of a broad, flattened, scoop-like process of which the apical part may either end in two separated or contiguous downwardly directed spines, processes or hooks, or it may be without spines and merely scoop-like or with a central, keel-like ridge dorsally and apically; middle bulb-like part of aedeagus usually small; lateral struts small; basal strut usually scarcely projecting posteriorly, bat-shaped, ham-shaped or boomerang-shaped. Ovipositor of females with a series of spines on each side, increasing in size from above to below and each with its apex bent sub-hook-like.

The male terminalia from dorsal aspect, epandrium removed, show a figure that is broad basally, narrowed apically, and while the epiphallus is large and quite wide basally, it is strongly attenuate regularly narrowing toward a point apically. It has a curious, backward-turned hooklike process on each side of the apex. From the lateral aspect the epandrium is triangular, not incised apically, although there is a lobelike extension at the top. The dististyle does not have a deep incision, although there is a very slight incision dorsally.

Material available for study: Numerous American species in my own collection, other species in the collections of the National Museum of Natural History and of the British Museum (Natural History). Prof. J. Timon-David of Marseille kindly sent me several European species for study. I also have representative material from South America and Australia.

Immature stages: Flies of this genus are parasites of nocturnal Lepidoptera. Some species attack coleopterous larvae of the family Tenebrionidae. See remarks under life histories.

Ecology and behavior of adults: The adults may be captured on a variety of flowers, especially composites. Painter (1926) records *Villa lateralis* Say from the flowers of *Tetranervis linearis*, *Lepadenia marginatum* (Pursh) Niewel, and from *Rhus* species. He states that they are found in Texas from March to November. I have taken species of *Villa* commonly on *Rhus* species and on sneeze weed, *Helianthemum tenuifolium* Linné. I have frequently found them hovering for long periods of time in forested areas, and I have also seen species apparently ovipositing in soil.

Distribution: Nearctic: *Villa adusta* (Loew), 1869 (as *Anthrax*); *aenea* (Coquillett), 1887 (as *Anthrax*); *agrippina* (Osten Sacken), 1887 (as *Anthrax*); *albicincta* Cole, 1923, s.l.; *albovittata* (Macquart), 1850 (as *Anthrax*, s.l.); *alternata* (Say), 1823 (as *Anthrax*) [= *albipictus* (Macquart), 1848 (as *Anthrax*), = *bastardi* (Macquart) 1840 (as *Anthrax*), = *consanguineus* (Macquart), 1840 (as *Anthrax*)], *alternata nigropictus* Cresson, 1916; *anna* (Coquillett), 1887 (as *Anthrax*, s.l.); *caprea* (Coquillett), 1887 (as *Anthrax*, s.l.); *cantor* (Coquillett), 1887 (as *Anthrax*, s.l.); *chromo-*

lepida Cole, 1923; *compressa* Painter, 1926; *conneza* (Macquart), 1855 (as *Anthrax*); *conessor* (Coquillett), 1887 (as *Anthrax*); *costata* (Say), 1824 (as *Anthrax*, s.l.); *faustina* (Osten Sacken), 1887 (as *Anthrax*); *fissa* (Bigot), 1892 (as *Anthrax*, s.l.); *flavocostalis* Painter, 1926; *fulviana* (Say), 1824 (as *Anthrax*); *fulviana nigricauda* Loew, 1869; *funicosta* Painter, 1962; *fumida* Coquillett, 1887; *gemella* (Coquillett), 1892 (as *Anthrax*, s.l.); *gracilis* (Macquart), 1840 (as *Anthrax*); *handfordi* Curran, 1935; *harveyi* (Hine), 1904 (as *Anthrax*); *hircina* (Coquillett, 1892 (as *Anthrax*); *hypomelaena* (Macquart), 1840 (as *Anthrax*); *inculta* (Coquillett), 1892 (as *Anthrax*, s.l.); *lateralis* (Say), 1823 (as *Anthrax*) [= *fulvipes* (Coquillett), 1887 (as *Anthrax*)]; *lateralis arenicola* (Johnson), 1908 (as *Anthrax*); *lateralis atra* Painter, 1926; *lateralis johnsoni* Painter, 1926; *lateralis nigra* Cresson, 1916; *lateralis semifulvipes* Painter, 1962; *levicula* (Coquillett), 1894 (as *Anthrax*, s.l.); *livia* (Osten Sacken), 1887 (as *Anthrax*); *meridionalis* Cole, 1923, s.l.; *miscella* (Coquillett), 1887 (as *Anthrax*, s.l.); *molitor* (Loew), 1869 (as *Anthrax*); *moneta* (Osten Sacken), 1887 (as *Anthrax*); *mucorea* (Loew), 1869 (as *Anthrax*); *muscaria* (Coquillett), 1892 (as *Anthrax*); *nebulo* (Coquillett), 1887 (as *Anthrax*); *pretiosa* (Coquillett), 1887 (as *Anthrax*); *psamma* Cole, 1960, s.l. [= *arenicola* Cole, 1923, s.l., not Johnson]; *sabina* (Osten Sacken), 1887 (as *Anthrax*); *salebrosa* Painter, 1926; *serobiculata* (Loew), 1869 (as *Anthrax*); *shawii* (Johnson), 1908 (as *Anthrax*); *sini* Cole, 1923, s.l.; *sodom* (Williston), 1893 (as *Anthrax*, s.l.); *squaminigera* (Coquillett), 1892 (as *Anthrax*); *stenoazona* (Loew), 1869 (as *Anthrax*); *supina* (Coquillett), 1887 (as *Anthrax*); *teluris* (Coquillett), 1892 (as *Anthrax*, s.l.); *terrena* (Coquillett), 1892 (as *Anthrax*, s.l.); *vacans* (Coquillett), 1887 (as *Anthrax*); *vanduzeei* Cole, 1923, s.l.; *vestita* (Walker), 1849 (as *Anthrax*).

Neotropical: *Villa abbreviata* (Wiedemann), 1830 (as *Anthrax*); *albicincta* Cole, 1923; *albicollaris* Cole, 1934; *albifacies* (Rondani), 1863 (as *Anthrax*); *albisima* Oldroyd, 1938; *amasia* (Wiedemann), 1828 [= *vicinus* (Macquart), 1840 (as *Anthrax*)]; *ambigua* (Lynch Arribáizaga), 1878 (as *Anthrax*); *angulata* Brèthes, 1909; *antica* (Walker), 1852 (as *Anthrax*); *argentiflua* (Philippi), 1865 (as *Anthrax*); *argentina* Painter, 1933; *ariditata* Cole, 1923; *balteata* (Philippi), 1865 (as *Anthrax*); *barbiventris* (Rondani), 1868 (as *Anthrax*); *bellula* (Philippi), 1865 (as *Anthrax*); *binotata* (Macquart), 1846 (as *Anthrax*); *bipartita* (Jaenicke), 1867 (as *Anthrax*); *bistella* (Walker), 1850 (as *Anthrax*); *brachialis* (Thomson), 1869 (as *Anthrax*); *calogaster* (Philippi), 1865; *caloptera* (Philippi), 1865 (as *Anthrax*); *calvescens* (Philippi), 1865 (as *Anthrax*); *castanea* (Jaenicke), 1867 (as *Anthrax*); *ceria* (Williston), 1901 (as *Anthrax*); *chilensis* (Philippi), 1865 (as *Anthrax*); *chimaera* (Osten Sacken), 1887 (as *Anthrax*); *cinerea* Cole, 1923; *conclusa* (Walker), 1857 (as *Anthrax*); *connexa* (Bigot), 1856 (as *Anthrax*); *conopas* (Philippi), 1865 (as

Anthrax); *constituta* (Walker), 1852 (as *Anthrax*); *conveza* (Walker), 1857 (as *Anthrax*); *corrigiolata* (Rondani), 1863 (as *Anthrax*); *costalis* (Wiedemann), 1828 (as *Anthrax*); *crepuscularis* (Lynch-Arribáizaga), 1878 (as *Anthrax*); *cyadicus* (Osten Sacken), 1886 (as *Anthrax*); *curvirostris* (Thomson), 1869 (as *Anthrax*); *decemmacula* (Walker), 1857 (as *Anthrax*); *delicatula* (Walker), 1849 (as *Anthrax*); *detecta* (Walker), 1852 (as *Anthrax*) [= *bipenicillatus* (Bigot), 1892 (as *Anthrax*)]; *diana* (Williston), 1901 (as *Anthrax*); *diminutiva* (Macquart), 1846 (as *Anthrax*); *ditaenia* (Wiedemann), 1828 (as *Anthrax*); *divisa* (Walker), 1852 (as *Anthrax*); *dorsalis* (Walker), 1857 (as *Anthrax*); *duodecimpunctata* (Philippi), 1865 (as *Anthrax*); *durvillei* (Macquart), 1840 (as *Anthrax*); *edwardsi* Oldroyd, 1938; *ephebus* (Osten Sacken), 1886 (as *Anthrax*); *epilais* (Wiedemann), 1828 (as *Anthrax*); *eurrhinata* (Bigot), 1892 (as *Anthrax*); *eacisa* (Walker), 1852 (as *Anthrax*); *extremities* (Coquillett), 1902 (as *Anthrax*); *fenestrellus* (Wiedemann), 1828 (as *Anthrax*); *fenestralis* (Wiedemann), 1830 (as *Anthrax*); *festiva* (Philippi), 1865 (as *Anthrax*); *flavicincta* Cole, 1923; *flavipilosa* Cole, 1923; *fulvago* (Philippi), 1865 (as *Anthrax*); *fulvipeda* (Rondani), 1863 (as *Anthrax*); *funebis* (Macquart), 1840 (as *Anthrax*); *fusca* (Fabricius), 1805 (as *Cytherea*); *galathea* (Osten Sacken), 1886 (as *Anthrax*); *gayi* (Macquart), 1840 (as *Anthrax*); *gorgon* (Fabricius), 1805 (as *Anthrax*); [= *maimon* (Fabricius), 1805 (as *Anthrax*)]; *gradata* (Macquart), 1847 (as *Anthrax*); *hilaris* (Macquart), 1840 (as *Anthrax*); *hirsuta* (Williston), 1901 (as *Anthrax*); *hyalacra* (Wiedemann), 1828 (as *Anthrax*); *hyalinipennis* (Blanchard in Gay), 1852 (as *Anthrax*); *ignea* (Macquart), 1846 (as *Anthrax*); *imitans* (Schiner), 1868 (as *Argyrotaenia*); *inexacta* (Walker), 1857 (as *Anthrax*); *ingloria* (Philippi), 1865 (as *Anthrax*); *inordinata* (Rondani), 1863 (as *Anthrax*); *ioptera* (Wiedemann), 1828 (as *Anthrax*); *latifimbria* (Walker), 1852 (as *Anthrax*); *lelia* (Williston), 1901 (as *Stonyx*); *lemniscata* (Philippi), 1865 (as *Anthrax*); *lepidota* (Osten Sacken), 1887 (as *Anthrax*); *leucomachus* (Philippi), 1865 (as *Anthrax*); *leucothoa* (Wiedemann), 1830 (as *Anthrax*); *lineata* (Walker), 1857 (as *Anthrax*); *maria* (Williston), 1901 (as *Anthrax*); *melaleuca* (Wiedemann), 1828 (as *Anthrax*); *melanogaster* (Bigot), 1892 (as *Anthrax*); *mendozaana* Brèthes, 1909; *micromelaena* (Bigot), 1892 (as *Anthrax*); *midas* (Fabricius), 1805 (as *Anthrax*); *minerva* (Wiedemann), 1828 (as *Anthrax*); *miniata* Oldroyd, 1938; *moerens* (Philippi), 1865 (as *Anthrax*); *moneta* (Osten Sacken), 1887 (as *Hyalanthrax*); *murina* (Philippi), 1865 (as *Anthrax*); *mutua* (Walker), 1849 (as *Anthrax*); *nero* (Fabricius), 1805 (as *Anthrax*); *nigricosta* (Schiner), 1868 (as *Anthrax*); *nigrita* (Fabricius), 1775 (as *Bibio*); *nigrofimbriata* (Williston), 1901 (as *Anthrax*); *nitida* Cole, 1923; *nivea* Cole, 1923; *nudiuscula* (Thomson), 1869 (as *Anthrax*) [= *lateralis* (Thomson), 1869 (as *Anthrax*)]; *obliqua* (Macquart), 1834 (as *Anthrax*); *obscuripes* (Bigot), 1892 (as *Anthrax*);

thraæ); *orbitalis* (Williston), 1901 (as *Anthraæ*); *pallipes* (Bigot), 1892 (as *Anthraæ*); *peninsularis* Cole, 1923; *perimele* Wiedemann, 1828; *philippii* (Rondani), 1863 (as *Anthraæ*); *pleuralis* (Williston), 1901 (as *Anthraæ*); *pluricella* (Williston), 1901 (as *Anthraæ*); *polyphemus* (Wiedemann), 1821 (as *Anthraæ*); *porteri* Oldroyd, 1938; *praeterita* Oldroyd, 1938; *primitiva* (Walker), 1849 (as *Anthraæ*); *procedens* (Walker), 1852 (as *Anthraæ*); *propinqua* (Schiner), 1868 (as *Argyramoeba*); *pusio* (Macquart), 1840 (as *Anthraæ*); *pusio* (Philippi), 1865 (as *Anthraæ*); *quadricincta* (Rondani), 1863 (as *Anthraæ*); *quadricincta* (Philippi), 1865 (as *Anthraæ*); *quadrupunctata* Cole, 1923; *quinquepunctata* (Thomson), 1869 (as *Lepidanthraæ*); *rava* Painter, 1933; *recta* (Walker), 1852 (as *Anthraæ*); *reperita* (Walker), 1852 (as *Anthraæ*); *restituta* (Walker), 1852 (as *Anthraæ*); *ruficollis* (Bigot), 1892 (as *Anthraæ*); *sackeniana* (Williston), 1901 (as *Isopenthes*); *scylla* (Osten Sacken), 1887 (as *Anthraæ*); *sejüngenda* (Rondani), 1863 (as *Anthraæ*); *semitincta* (Schiner), 1868 (as *Anthraæ*) [= *semicinctus* (Bigot), 1892 (as *Glossista*), lapsus]; *solita* (Walker), 1857 (as *Anthraæ*); *sonorensis* Cole, 1923; *spiloptera* (Wiedemann), 1828 (as *Anthraæ*); *stheno* (Wiedemann), 1828 (as *Anthraæ*); *subaequalis* (Lynch Arribáizaga), 1878 (as *Anthraæ*); *tenuirostris* (Macquart), 1849 (as *Anthraæ*); *tincta* (Thomson), 1869 (as *Anthraæ*); *translata* (Walker), 1852 (as *Anthraæ*); *trifigurata* (Walker), 1860 (as *Anthraæ*); *trimaçula* (Walker), 1849 (as *Exoprosopa*); *trimaçulata* (Macquart), 1848 (as *Anthraæ*); *una* Oldroyd, 1938; *vastitatis* Cole, 1923; *verdensis* Oldroyd, 1938; *vicina* (Macquart), 1846 (as *Anthraæ*); *antipoda*, n.n., for *vicina* (Blanchard in Gay), 1852, not *vicina* (Macquart), 1846; *viduata* (Loew), 1860 (as *Anthraæ*); *villicus* (Philippi), 1865 (as *Anthraæ*); *vitrivennis* (Philippi), 1865 (as *Anthraæ*); *vulpecula* (Philippi), 1865 (as *Anthraæ*).

Palaeartic: *Villa abaddon* (Fabricius), 1794 (as *Anthraæ*) [= *abaddon* (Meigen), 1820 (as *Anthraæ*)] = *concinus* (Meigen), 1820 (as *Anthraæ*); *aegyptiaca* (Macquart), 1840 (as *Anthraæ*); *albida* Becker, 1916; *albiventris* Frey, 1936; *albula* (Loew), 1869 (as *Anthraæ*) [= *quinta* Becker, 1916]; *arabica* (Macquart), 1840 (as *Anthraæ*); *atricauda* Austen, 1937; *baluchiana* Brunetti, 1920; *bicingulata* (Macquart), 1840 (as *Anthraæ*); *bimaçula* (Walker), 1849 (as *Anthraæ*); *bivirgata* Austen, 1937; *bizonata* Becker, 1916; *bombiformis* Becker, 1916; *brunnea* Becker, 1916; *ceballosi* Rubio, 1959; *cingulata* (Meigen), 1804 (as *Anthraæ*) [= *hottentotta* Jaennicke, 1867, = *cingulatus* (Zetterstedt), 1842, not Meigen (as *Anthraæ*)]; *cingulum* (Wiedemann in Meigen), 1820 (as *Anthraæ*); *circumdata* (Meigen), 1820 (as *Anthraæ*); [= *cingulatus* (Walker not Meigen), 1851 (as *Anthraæ*), = *flavus* (Curtis not Meigen), 1824 (as *Anthraæ*)] = *hottentottus* (Schellenberg), 1803 (as *Anthraæ*)] = *stoechades* (Jaennicke), 1867 (as *Anthraæ*), *circumdata algeciras* Strobl, 1909, *circumdata fulvimaçulata* Abreu, 1926; *claretta*, n.n., for *claripennis* Becker, 1923; *claripennis*

(Kowarz), 1867 (as *Anthraæ*); *clarissima* (Loew), 1857 (as *Anthraæ*) [= *cyprignus* (Rondani), 1863 (as *Anthraæ*)] = *combinata* (Walker), 1857 (as *Anthraæ*), *decipula* Austen, 1937; *distincta* (Meigen), 1838 (as *Anthraæ*); *doriae* Bezzi, 1922; *euzona* (Loew), 1869 (as *Anthraæ*); *fallax* Austen, 1937; *fasciata* (Meigen), 1804 (as *Anthraæ*); *fasciculata* Becker, 1916; *fasciventris* (Macquart), 1849 (as *Anthraæ*) [= *fusciventris* Loew, 1860, lapsus]; *haesitans* Becker, 1916; *halteralis* (Kowarz), 1883 (as *Anthraæ*) [= *circumdata* (Meigen), 1820]; *hottentotta* (Linné), 1758 (as *Musca*) [= *flavus* (Meigen), 1820 (as *Anthraæ*), = *perfecta* Becker, 1906, = *suprema* Becker, 1916]; *hottentotta modesta* (Meigen), 1820 (as *Anthraæ*); *humilis* (Ruthe), 1831 (as *Anthraæ*) [= *mucidus* (Zeller), 1840 (as *Anthraæ*)] = *insignis* Austen, 1937; *ivion* (Fabricius), 1794 (as *Anthraæ*); *laevis* Becker, 1915 [= *inconstans* Becker, 1916]; *latifascia* (Walker), 1857 (as *Anthraæ*); *leucostoma* (Meigen), 1820 (as *Anthraæ*); *limbata* (Coquillett), 1898 (as *Anthraæ*); *longipennis* (Macquart), 1840 (as *Anthraæ*); *longitarsis* (Becker), 1902 (as *Anthraæ*); *luculenta* Ségué, 1941; *marginalis* (Wiedemann in Meigen), 1820 (as *Anthraæ*); *melanura* (Loew), 1869 (as *Anthraæ*); *micrargyra* (Walker), 1871 (as *Anthraæ*); *multibalteata* Austen, 1936; *muscaria* (Pallas in Meigen), 1818 (as *Anthraæ*); *nigriceps* (Macquart in Webb and Berthelot), 1838 (as *Anthraæ*); *nigriceps abdominalis* Abreu, 1926; *nigrifrons* (Macquart in Webb and Berthelot), 1838 (as *Anthraæ*); *niphobleta* (Loew), 1869 (as *Anthraæ*) [= *nana* Becker, 1916]; *nomas* (Eversmann), 1854 (as *Anthraæ*); *obscura* (Weber), 1801 (as *Anthraæ*); *occulta* (Wiedemann in Meigen), 1820 (as *Anthraæ*); *ovata* (Loew), 1869 (as *Anthraæ*); *pallumbii* Rondani, 1877; *paniscus* (Rossi), 1790 (as *Bibio*) [= *bimaçulatus* (Macquart), 1834 (as *Anthraæ*)] = *cingulatus* (Meigen), 1820 (as *Anthraæ*)] = *hottentottus* (Walker not Linné), 1849 (as *Anthraæ*)] = *perfecta* (Becker), 1906 (as *Anthraæ*); *persica* (Macquart), 1840 (as *Anthraæ*); *plagiata* (Walker), 1849 (as *Anthraæ*); *punctata* (Macquart), 1834 (as *Anthraæ*) [= *punctulatus* (Macquart), 1835 (as *Anthraæ*); *punctum* (Loew), 1854 (as *Anthraæ*); *pygarga* (Loew), 1868 (as *Anthraæ*); *quinquefasciata* (Wiedemann in Meigen), 1820 (as *Anthraæ*) [= *blanda* Loew, 1869, = *cana* Meigen, 1804, = *inquieta* Becker, 1916, = *mus* Becker, 1916]; *ruficeps* (Macquart), 1840 (as *Anthraæ*); *scrutata* (Wiedemann in Meigen), 1820 (as *Anthraæ*); *sardous* (Macquart), 1849 (as *Anthraæ*); *satanas* Becker, 1916; *senecio* (Loew), 1869 (as *Anthraæ*); *squamifer* (Jaennicke), 1867 (as *Anthraæ*); *stenoazona* (Loew), 1869 (as *Anthraæ*) [= *disjuncta* Becker, 1916]; *suffusa* (Walker), 1849 (as *Anthraæ*); *svenhedini* Paramonov, 1934; *syphax* (Fabricius), 1798 (as *Anthraæ*); *tankervina* (Bigot), 1892 (as *Anthraæ*); *tashkentica* Paramonov, 1925; *tenuis* (Walker), 1871 (as *Anthraæ*); *tomentosa* Becker, 1916; *varipennis* (Macquart), 1849 (as *Anthraæ*); *ventruosus* (Loew), 1869 (as *Anthraæ*); *venusta* (Meigen), 1820 (as *Anthraæ*) [= *dolosus* (Jaennicke), 1867 (as *An-*

thrax, =*margaritifer* (Dufour), 1833 (as *Anthrax*), =*turbidus* (Loew), 1869 (as *Anthrax*); *vitripennis* (Loew), 1860 (as *Anthrax*).

Ethiopian: *Villa albescens* (Loew), 1860 (as *Anthrax*); *anthophoroides* Hesse, 1956; *apiformis* Hesse, 1956; *apparens* (Walker), 1852 (as *Anthrax*); *argentina* Bezzi, 1921; *aspiculata* Hesse, 1956; *atrisquama* Bezzi, 1924; *aurocincta* (Bigot), 1892 (as *Anthrax*); *biflexa* Loew, 1852; *biguttata* Macquart, 1834; *bravae* Bezzi, 1922; *candidata* Bezzi, 1924; *chionalis* Hesse, 1956; *chrysothrix* Bezzi, 1924; *commiles* (Walker), 1857 (as *Anthrax*); *dissimilis* Hesse, 1956; *dizona* (Loew), 1860 (as *Anthrax*); *eucnemis* François, 1961; *fenestralis* (Macquart), 1840 (as *Anthrax*); *filicornis* Hesse, 1956; *flammigera* (Walker), 1849 (as *Anthrax*); *flavalis* Hesse, 1956; *flavescens* (Loew), 1860 (as *Anthrax*); *flavipes* (Loew), 1860 (as *Anthrax*); *fulvipleura* Hesse, 1956; *gariepina* Hesse, 1956; *harroyi* François, 1961; *hybrida* Hesse, 1956; *kaokoensis* Hesse, 1956; *karasana* Hesse, 1956; *karoensis* Hesse, 1956; *lasia* (Wiedemann), 1824 (as *Anthrax*); *leptopus* (Thomson), 1869 (as *Anthrax*); *leucochila* Bezzi, 1921 [= *leucostomus* (Weidemann), 1821 (as *Anthrax*)]; *leucoproctus* (Loew), 1860 (as *Anthrax*); *lloydii* Austen, 1914; *loewii* Hesse, 1956; *madagascariensis* (Macquart), 1847 (as *Anthrax*); *nilotica* (Jaenicke), 1867 (as *Anthrax*); *niphobletoides* Hesse, 1956; *nivearia* Hesse, 1956; *pachystyla* Hesse, 1956; *paniscoides* Bezzi, 1912; *phaeotaenia* Bezzi, 1922; *punctulata* (Macquart), 1840 (as *Anthrax*); *pusilla* (Wiedemann), 1821 (as *Anthrax*); *searfasciata* (Wiedemann), 1821 (as *Anthrax*); *sokotrae* (Ricardo in Forbes), 1903 (as *Anthrax*); *submacula* (Walker), 1849 (as *Anthrax*); *terminus* (Walker), 1849 (as *Anthrax*); *turneri* Hesse, 1956; *unifasciata* (Macquart), 1840 (as *Anthrax*); *validicornis* Bezzi, 1924.

Oriental: *Villa abeilla*, n.n., for *Anthrax antecedens* (Walker), 1859, not (Walker), 1852 (as *Anthrax*, U.S.); *absalon* (Wiedemann), 1824 (as *Anthrax*); *albofulva* (Walker), 1852 (as *Anthrax*); *angustata* (Dolschall), 1858 (as *Anthrax*); *antecedens* (Walker), 1860 (as *Anthrax*); *aperta* (Walker), 1852 (as *Anthrax*); *argenticulatus* (Walker), 1857 (as *Anthrax*); *aterrima* (Dolschall), 1858 (as *Anthrax*) [= *proferens* Walker, 1860]; *aureohirta* Brunetti, 1909; *aygula* (Fabricius), 1805 (as *Anthrax*); *carbonaria* Walker, 1852 (as *Anthrax*); *clara* (Walker), 1852 (as *Anthrax*); *confirmata* (Walker), 1861 (as *Anthrax*); *congrua* (Walker), 1852 (as *Anthrax*); *demonstrans* (Walker), 1860 (as *Anthrax*); *devecta* (Walker), 1861 (as *Anthrax*); *dia* (Wiedemann), 1824 (as *Anthrax*); *emarginata* (Macquart), 1840 (as *Anthrax*); *emissa* (Walker), 1864 (as *Anthrax*); *emittens* (Walker), 1861 (as *Anthrax*); *instituta* (Walker), 1852 (as *Anthrax*); *leucopyga* (Macquart), 1840 (as *Anthrax*); *limpida* (Walker), 1852 (as *Anthrax*); *manifesta* (Walker), 1852 (as *Anthrax*); *melasoma* (Wulp), 1882 (as *Anthrax*); *nigricostalis* (Guérin-Ménéville), 1838 (as *Anthrax*); *praedicans* (Walker), 1860 (as *Anthrax*); *pretendens*

(Walker), 1860 (as *Anthrax*); *satellitica* (Walker), 1857 (as *Anthrax*); *semifusata* Brunetti, 1920; *semihyalina* (Meijere), 1907 (as *Anthrax*); *terminalis* (Wulp), 1868 (as *Anthrax*) [= *leucostigma* Wulp, 1898]; *trimaculata* (Wulp), 1868 (as *Anthrax*); *troglydota* (Fabricius), 1775 (as *Bibio*) [= *hyalinus* Wiedemann, 1821, = *lucens* Walker, 1852].

Australian: *Villa albata* Roberts, 1928; *albirufa* (Walker), 1857 (as *Anthrax*); *albobasalis* Roberts, 1928; *alternans* (Macquart), 1849 (as *Anthrax*); *alterna* (Walker), 1849 (as *Anthrax*); *angularis* (Thomson), 1869 (as *Anthrax*); *apicifera* (Walker), 1865 (as *Anthrax*); *aprica* Roberts, 1928; *argentipennis* White, 1917; *australis* (Walker), 1852 (as *Anthrax*); *brunea* Roberts, 1928; *commista* (Macquart), 1849 (as *Anthrax*); *consimilis* Thomson, 1869 (as *Anthrax*); *flavola* (Macquart), 1849 (as *Anthrax*); *fumea* Roberts, 1928; *incisa* (Macquart), 1847, (as *Anthrax*); *incompta* (Walker), 1849 (as *Anthrax*); *maculata* (Macquart), 1846 (as *Anthrax*); *marginata* (Walker), 1852 (as *Anthrax*); *minor* Macquart, 1849 (as *Anthrax*); *nigricosta* (Macquart), 1849 (as *Anthrax*); *obscura* Macquart, 1846; *pellucida* (Walker), 1852 (as *Anthrax*); *proconica* Hardy, 1942 [= *conica* (Macquart), 1849 (as *Anthrax*)]; *quinqueguttata* Roberts, 1928; *rava* Roberts, 1928; *resurgens* (Walker), 1849 (as *Anthrax*); *semimaculata* (Walker), 1849 (as *Anthrax*); *serpentina* (Walker), 1849 (as *Anthrax*); *sobriola* (Walker), 1857 (as *Anthrax*); *subobscura* Hardy, 1942 [= *obscurus* Macquart, 1846]; *subsenex* (Walker), 1857 (as *Anthrax*); *trivincta* Roberts, 1928; *varipennis* Roberts, 1928; *vitrea* (Walker), 1852 (as *Anthrax*); *lucidus* Walker; *leucotelus* Walker.

Oceania: *Villa basalis* (Macquart), 1855 (as *Anthrax*); *biappendiculata* Macquart, 1855.

Ignota Patria: *Villa brunipennis* Macquart, 1840; *confluens* (Macquart), 1840 (as *Anthrax*); *diana* (Walker), 1849 (as *Anthrax*); *fervida* (Walker), 1849 (as *Anthrax*); *fumipennis* (Wiedemann), 1828 (as *Anthrax*); *fuscicostata* (Macquart), 1846 (as *Anthrax*); *gnata* (Walker), 1852 (as *Anthrax*); *ignifera* (Walker), 1852 (as *Anthrax*); *illata* (Walker), 1852 (as *Anthrax*); *insularis* (Walker), 1849 (as *Anthrax*); *noctiluna* (Walker), 1849 (as *Anthrax*); *notabilis* (Macquart), 1840 (as *Anthrax*); *purpurata* (Wiedemann), 1828 (as *Anthrax*); *reducta* (Walker), 1852 (as *Anthrax*); *semilimpida* (Wiedemann), 1828 (as *Anthrax*); *sextotata* (Macquart), 1855 (as *Anthrax*); *subannulus* (Walker), 1849 (as *Anthrax*); *succedens* (Walker), 1852 (as *Anthrax*); *trivittata* (Macquart), 1834 (as *Anthrax*).

Genus *Astrophanes* Osten Sacken

FIGURES 172, 395, 660, 666, 927, 928

Astrophanes Osten Sacken, Biologia Centrali-Americana, Dipt., vol. 1, p. 106, 1886. Type of genus: *Astrophanes adonis* Osten Sacken, 1886, by monotypy.

Queer little flies of black color, the males with the last half of the abdomen covered with dense, silvery or creamy-white pile laid down in a mat in which the shining hairs are longitudinally placed. The head is large, subglobular, distinctly wider than the thorax. The front, except a smaller, upper, triangular part, is densely covered with shining white hair; this hair is appressed forward and only silvery in appearance when viewed from above. Wings hyaline.

In addition to the general appearance described above there are several other noteworthy characters. These small flies have the male eyes separated by less than the width of one ocellus. The occiput is unusually short and poorly developed but there is a shallow indentation and a distinct bisecting line. The adjacent collar of pile on the anterior mesonotum is high, conspicuous in contrast to the remaining pile. The face is short, nearly vertical, not protruding, but rounded from side to side. The antennae are quite short; the third segment is so short that Osten Sacken described it as a mere disc and its short stylar portion ends in a minute bristle. The anal cell is closed and bears a short stalk.

The type-species ranges from northern Mexico into Arizona and Utah on the west, into Texas and Kansas on the east; I have collected it in several localities. Brèthes (1909) described the species *andina* from Mendoza which he placed here.

Length: 4 to 5 mm.

Head, lateral aspect: Large and subglobular. The occiput, while relatively short, shortens still more toward the vertex, especially in the male. And the pile of the occiput in both sexes is scanty, fine, and erect near the vertex but flat-appressed, matted, and scalelike at and above the indentation. Because the very deep occipital cup or recess is so large the short, dense, silvery, marginal fringe is relatively close to the eye margin, especially in the male; in the female the occiput is wider and more extensive. The front is quite extensive and convex, almost or completely level with the eye, scarcely protruding even at the antenna. It is very slightly convex from side to side. The male front has dense, matted, subappressed, silvery scales and a small, upper triangle with fine, erect, black hairs. Female front with broad, silvery scales in a narrow band just in front of the antennae and in a small, lateral tuft near the middle. The face is prominent, extensive vertically, and extended forward at the oral recess, a distance fully equal the length of the antennal style. It is somewhat shorter beneath the antenna and is rather more protrusive in the female. The pile of the face consists of a few, scattered, silvery scales, a tuft of similar scales along the eye margin representing an extension from the front and reaching halfway down the face. Also the face has scattered, fine, erect blackish and whitish hairs. The eye is extremely large. The posterior margin has a moderately deep, acute indentation of little width or breadth, with a small sunken

triangle from which proceeds a long, bisecting line directed forward almost half the length of the eye. Upper facets strongly enlarged. The eye is almost as long as high.

The proboscis is small, short, slender, the labellum small, short oval, not extending to the apex of the oral recess. Palpus quite slender, clavate, and pointed apically and about half as long as the proboscis. The antennae are attached at the middle of the head, and are medium sized, but exceptionally short on all three segments. The very short first segment has a lateral fringe of coarse, bristly pile extending from the middle above almost to the ventral surface. The third segment is much wider medially than the second segment and has the form of a flat, short disc with rounded edges. It bears subdorsally a short, thick style in length perhaps as much as the width of the basal disk.

Head, anterior aspect: Head considerably wider than the thorax. In the male the eyes are linearly separated by a little less than the width of the anterior ocellus. The upper posterior corners of the eye are broadly rounded and each eye is more or less recessed forward so that, viewed from above, the posterior eye margin is not plane. The front in the male is wide at the antenna, the whole front forming a very short isosceles triangle. In the female the eyes are separated by rather more than the width of the second antennal segment and less than the third. Ocellar tubercle moderately high, the ocelli set in an equilateral triangle at the posterior eye corners. The antennae are quite widely separated by nearly twice the amount of the distance from antenna to eye. The oral recess is small, long, and narrow with a deeper medial groove or pocket, extending to the apex. The eye margins almost reach to the wall of the oral recess but recede ventrally so that the gena is in evidence only at the bottom of the eye. There is a quite linear fissure along the eye margin, midway between the antenna and the base of the proboscis. Viewed from above the lobes of the occiput are shallow and narrowly separated, more strongly divergent behind the vertex.

Thorax: Shining black with more or less scattered, erect, slightly flattened hairs over the mesonotum and with tufts of longer, distinctly scaliform pile on humerus and notopleuron. The anterior collar is composed of a single row of long, stiff, white hairs. Scutellum subtriangular, bluntly pointed apically, slightly rounded near the base on each side. The mesopleuron has only a little pile near the top, and it is stiff and forms scaliform bristles. Pteropleuron with a few bristly hairs, hypopleuron bare, but metapleuron with an extensive tuft of bristly hair. Scales of squamae broad, conspicuous and white.

Legs: Rather small, black in color. Anterior femur with a few minute setae ventrally, middle femur with a conspicuous fringe of slender, bristly hairs postero-ventrally. However, the hind femur has only 4 to 6 very slender, oblique bristles ventrally. Anterior tibiae

smooth above, the tarsi small. Middle tibia with 2 or 3 bristles anterodorsally, but with 7 to 9 considerably stouter, though slender, oblique, sharp bristles posterodorsally. Middle basal tarsi obliquely spiculate. Hind tibia with 3 or 4 small ventral bristles but with 12 to 14 more conspicuous, longer, stout yet slender bristles posterodorsally. Claws small, slightly curved, pulvilli absent. All the femora and tibiae and the tarsi as well covered with flat-appressed, iridescent scales.

Wings: Relatively large, quite broad, completely hyaline, all the posterior cells widely open. There are 2 submarginal cells; the second vein has a gentle bend near the apex so that the marginal cell is gently rounded below apically. The anterior crossvein enters the middle of the discal cell. The second vein arises opposite it rectangularly, usually with a rounded bend, but sometimes with a rectangular bend. Anal cell closed in the margin or with a short stalk. Alula large, ambient vein complete. Basal comb wide with stiff black setae.

Abdomen: At the base as wide as the thorax, at the end of the third tergite even wider. Males with erect, coarse, brushy pile laterally on the first tergite and with a band of whitish, subappressed pile across the base of the second tergite, which is somewhat scaliform and is apt to be more conspicuous in the females and matted and appressed. In males the remainder of the second tergite and all of the third tergite are covered with small purplish to greenish-black scales that are fully appressed, but with the fourth and remaining tergites covered by a dense, appressed mat of silvery or sometimes cream-colored scales, extending over the posterior margin and each band overlapping and the last band forming a hood over the small, recessed, asymmetrical genitalia. Female with shorter, yellowish scales along the base of all the tergites but forming no conspicuous silvery mat. Remainder of the female tergites with the small, greenish or coppery scales.

The male terminalia from dorsal aspect, epandrium removed, show a basally wide, apically narrowing structure. The basal part of the aedeagus is very large and bulb-shaped, narrowing apically where it reaches under the remarkably prominent, wide, tongue-shaped epiphallus. Dististyli small, attenuate apically with a hooklike divergent process. From the lateral aspect, the basistyle is long and stout but the epandrium is relatively short and is subquadrate, but with prominent, conical, downturned basal lobes.

Material available for study: The type-species collected by author and wife in New Mexico, in 1926.

Immature stages: Unknown.

Ecology and behavior of adults: These flies are generally found resting on the sandy soil of semiarid regions. I have collected them on several occasions in the southwestern United States.

Distribution: Neotropical: *Astrophanes adonis* Osten Sacken, 1886; *andinus* Brèthes, 1909.

Genus *Chrysanthrax* Osten Sacken

FIGURES 170, 179, 663, 936, 937

Chrysanthrax Osten Sacken, Biologia Centrali-Americana, Dipt., vol. 1, p. 121, 1886. Type of genus: *Anthrax cypris* Meigen, 1820, as *Anthrax fulcohirta* Wiedemann. Designated by Coquillett, p. 523, 1910, the fourth of 4 species.

Small to medium-sized, *Villa*-like flies in which the oblique basal band or triangle of the wing is sometimes dark brown and sharply delimited, as in the type-species and a few other species but is more often pale, much reduced in color, more yellowish, the margin diffuse or reduced further to a few, small spots about crossveins and basal furcations.

Also, in this genus, the pile is uniformly short and entirely or almost entirely flat-appressed; margins of segments of the abdomen without tufts or extensive pile; general color of pile yellowish or golden, sometimes straw-colored or whitish, doubtless providing the name selected by the author of the genus.

The proboscis is slender, the labellum thin vertically, its shape lanceolate ovate and usually protruding a short distance beyond the oragenal recess. Anterior tibia quite smooth, reduced in size; pulvilli absent. The extent of contact of the fifth vein with the discal cell varies from short to commonly punctiform.

Chrysanthrax as at present known is characteristic of the southwestern United States: 17 of the 22 species included in the genus by Painter and Painter (1965) are from California; 2 or 3 species are found in the eastern and southeastern United States.

Length: 6 to 15 mm.

Head, lateral aspect: Head hemiglobular, the occiput strongly developed, shorter below, and the pile consists of appressed scaliform hairs, and a central fringe which becomes denser dorsally. The eye is large, the posterior indentation is quite shallow, although extensive above and below, and the bisecting line at the mid-point of the indentation extends inward over the eye for a considerable distance. The eye often has a strong greenish reflection. The front in profile is slightly protuberant or raised over the eye margin and covered with scattered, fine, erect, bristly pile. And in addition either with suberect, scaliform hairs or with numerous, slender, bright-colored scales. Similar hair and scales extend downward rather densely over the middle and sides of the face and form a loose fringe over the margin on the anterior part of the oral cup. The face is characteristically extended forward as a sharp, or sometimes lightly blunted triangle or cone, but not so sharp and extensive as in *Dipalta* Osten Sacken or *Stonyx* Osten Sacken. The proboscis is slender and may be confined to the oral cup or the labellum may extend beyond the cup. Palpus short and cylindrical with a scanty ventral fringe of hairs. The antennae are attached slightly above the middle of the head. They are small and slender. A rather tiny first segment is almost twice as long as wide, wider apically with

numerous, short, fine setae on all sides, except ventrally. The second segment is small and beadlike, nearly as long as wide, with minute setae. The third segment is elongate conical, tapering into a slender style which occupies the outer half of the segment and bears a minute spine at the apex.

Head, anterior aspect: A little narrower than the posterior width of the mesonotum, nearly circular from the front. The eyes are separated by slightly more than the length of the first two antennal segments and by about 3 times the width of the ocellar tubercle. The ocellar tubercle is quite small, almost equilateral, sometimes nearly twice as long as wide. Front covered with pollen in addition to the pile. The antennae are quite widely separated and are not more distant from the eye margin than the length of the first antennal segment. They may be even closer. The oragenal cup is long, rather narrow, deep posteriorly with strongly thickened sides along the middle, and the recess is distinctly narrowed anteriorly. The oral cup extends downward below the eye margin to a moderate extent, most of which may be considered gena. Anteriorly the gena is linear, shelving inward for an extensive distance as a deep, conspicuous fissure. Laterally there is a bare circling band reaching from the eye margins to each antenna, on which pile is absent. Viewed from above the occipital lobes are extensive and nearly horizontal, although they slope downward to some extent. The ocellar tubercle is set a considerable distance forward from the slightly rounded posterior eye corners.

Thorax: Slightly wider posteriorly, the mesonotum opaque, pollinose, with blackish ground color, though generally lighter along the lateral margin, postalar callosity, and scutellum. The pile, except as denuded, is comparatively dense, fine, appressed, and scaliform. The anterior collar is dense and rather extensive in depth; it is comparatively short, but extends backward grading into the mesonotal pile. Notopleural bristles weak, postalar callosity with fine bristles or as many as 4 rather strong, long bristles. The rather flattened scutellum bears a fringe of numerous, rather fine bristles. There are dense tufts of long coarse pile on the propleuron and the whole of the mesopleuron and metapleuron. There is some scattered, stiff pile on the pteropleuron and a tuft of hair beneath the haltere. Plumula likewise pilose. Hypopleuron bare, except for 3 or 4 hairs above the posterior coxa. There is a fringe of short stubby hair on the spiracle. Squamal scales short.

Legs: Slender and weak, especially the anterior pair. Anterior tibia smooth. The tarsus has only fine hair beneath. Middle femur with 2 or 3 rather stout bristles at the middle or beyond. Hind femur with 5 to 7 rather strong bristles ventrally. Middle and hind tibia with a few sharp, rather slender, oblique bristles in 4 rows. The hind tibia has 6 or 7 bristles anterodorsally, the same number posterodorsally, 5 or 6 anteroventrally, and the same number smaller and finer posteroventrally. The more minute setate bristles have

been omitted from this count. Hind tarsi strongly attenuate, the terminal segments are minute and slender, but setate below. Claws small, fine, very slightly curved, pulvilli absent. Anterior claws quite minute.

Wings: The wings vary from obliquely and irregularly but sharply reddish brown on the basal half or more as in the type-species to a pattern somewhat more common where the color is much more dilute and pale, but where there are smaller diffuse, darker spots on the crossveins. There are only 2 submarginal cells. The anterior crossvein enters the discal cell at or often beyond the middle of that cell and the second vein arises at or before the anterior crossvein. The contact of the discal cell with the fourth posterior cell is characteristically punctiform or nearly so. Anal cell open but only to a moderate extent. Alula moderately wide. Ambient vein complete. Costa rather strongly expanded at the base, but with minute setae and the costal hook sharp and thornlike.

Abdomen: Short oval. Generally wider than the thorax at least at the base. Color black, but usually with the sides of the tergites broadly and sometimes very broadly reddish yellow or orange and the sternites similarly pale, except in the middle. The pile is dense, flat-pressed, and distinctly scaliform or even forming lanceolate scales; generally some shade of yellow, orange, or red, there may be a few black scales intermixed and commonly there are some scattered black hairs along the posterior margins of the tergites, quite fine and suberect, or even entirely erect in the middles of the tergites, but becoming a little more numerous and conspicuous near the lateral margins of the tergites. The dense pile on the sides of the first tergite is conspicuous and blunt-tipped and often extends backward over the sides of the second tergite. There are 7 tergites visible from above. The last sternite may form a clasperlike lappet on each side. The acanthophorites have a fringe of 5 red spines on each side. Male terminalia large but rather strongly recessed with a tendency to be enclosed by sternal lappets.

The male terminalia from dorsal aspect, epandrium removed, show a broad, wide base, the whole figure narrowing apically. Dististyli are small, the epiphallus prominent and spade-shaped apically. From the lateral aspect, the small dististylus is incised dorsally and apically, with the apex sharp, hook-shaped and turned upward. It arises dorsoapically from the extensive basistylus. The epiphallus forms a curious, narrow, slender structure with a small dilated cap at the apex above and a triangular process below. The epandrium is odd; it forms a large, long, curved structure somewhat like an inverted U with the basal arm strongly extended downward.

Material for study: Many species from the southwestern United States, collected by the author and his wife on various expeditions—1926, 1949, 1954, 1959, and 1962.

Immature stages: Larvae of these species where the habits are known attack white grubs.

Ecology and behavior of adults: The adults are abundant and readily captured on low-growing flowers, especially composites. They may be found in temperate regions of high rainfall as well as in semiarid country.

Distribution: Nearctic: *Chrysanthrax adumbratus* (Coquillett), 1887 (as *Anthrax*); *altus* (Tucker), 1907 (as *Anthrax*); *arenosus* (Coquillett), 1892 (as *Anthrax*); *arizonensis* (Coquillett), 1887 (as *Anthrax*); *cinefactus* (Coquillett), 1892 (as *Anthrax*); *crocinus* (Coquillett), 1892 (as *Anthrax*); *cypris* (Meigen), 1820 (as *Anthrax*) [= *conifacies* (Macquart), 1850 (as *Anthrax*), = *fulvohirta* (Wiedemann), 1821 (as *Anthrax*)]; *dispar* (Coquillett), 1887 (as *Anthrax*); *edititius* (Say), 1829 (as *Anthrax*) [= *impiger* (Coquillett), 1887 (as *Anthrax*), = *sabulosa* (Coquillett), 1892 (as *Anthrax*)]; *eudorus* (Coquillett), 1887 (as *Anthrax*); *hircinus* (Coquillett), 1892 (as *Anthrax*); *junctura* (Coquillett), 1887 (as *Anthrax*); *lepidotoides* Johnson, 1919 [= *lepidota*, authors, not Osten Sacken]; *mirus* (Coquillett), 1887 (as *Anthrax*); *nebulosus* (Coquillett), 1894 (as *Anthrax*); *pallidulus* (Coquillett), 1894 (as *Anthrax*); *scitulus* (Coquillett), 1887 (as *Anthrax*); *tantillus* (Coquillett), 1892 (as *Anthrax*); *turbatus* (Coquillett), 1887 (as *Anthrax*) [= *comparata* (Tucker), 1907 (as *Anthrax*)]; *vanus* (Coquillett), 1887 (as *Anthrax*); *variatus* (Coquillett), 1892 (as *Anthrax*); *vulpinus* (Coquillett), 1892 (as *Anthrax*).

Neotropical: *Chrysanthrax astarte* (Wiedemann), 1830 (as *Anthrax*).

Genus *Cyananthrax* Painter

FIGURES 175, 373, 675, 938, 939, 940, 941

Cyananthrax Painter, Journ. Kansas Ent. Soc., vol. 32, p. 73, 1959. Type of genus: *Anthrax cyanoptera* Wiedemann, 1830, by original designation.

Rather large, peculiar flies of moderately lengthened abdomen, of brown or blue-black coloration, which have very large, broad, uniformly dark wings and the alula absent or quite linear. The face is quite conical, the proboscis confined to the oral recess, and the front tibiae are smooth; pulvilli vestigial. These characters are sufficient to identify this genus which is probably distantly related to *Poecilanthrax* Osten Sacken; like the latter genus *Cyananthrax* Painter has a distally directed spur vein from the lower outer corner of the discal cell. Unlike *Poecilanthrax* Osten Sacken the discal cell is separated from the fourth posterior cell by the presence of the posterior crossvein.

Only one species is known. I collected it around Tepotzlan in southern Mexico.

Length: 9 to 11 mm.; of wing 11 to 15 mm.

Head, lateral aspect: Head hemiglobular with strongly developed occiput, except near the bottom of

the head where it is much shorter. Occipital pile bristly, subappressed in a forward direction. The central fringe about the exceptionally large postoccipital recess is dense and short. The front is slightly raised, covered with sparse, bristly hairs of no great length, especially dorsally and toward the sides. These hairs are slightly curled forward and the lower middle part of the front is covered with some appressed, short bristly hair. The face is rather acutely conical; it extends forward in a long triangle almost as far as the apex of the antennal style. The eye is slightly reniform. The posterior indentation is rather shallow but quite long vertically. The eye bulges upward and away from the occiput on the dorsal third. Upper facets are small, the anterior facets only slightly more enlarged. The face bears scattered, strongly appressed, short bristly hairs and at the peak of the face above the narrowed oral cup, there are 3 groups of short, stout, matted bristles. The proboscis is comparatively slender and is confined to the oral recess; its lower surface is grooved. The filiform palpus is only a fourth as long as the proboscis but with 6 or 7 moderately long, quite slender, bristly hairs along its ventral lateral margin.

The antennae are attached at the upper third of the head. The first segment is a little more than twice as long as wide. The second segment is short and annulate, quite plane apically. At most it is as long as wide and the third segment is not attached tightly. The third segment is elongate conical with nearly plane base beginning to narrow just before the middle into an apically very slender style with very minute spine at tip. The whole third segment is very little longer than the first two segments combined. The first segment bears some short, shaggy bristly pile.

Head, anterior aspect: The head is a little more narrow than the posterior part of the thorax, nearly circular from the front. Not quite as wide as high because of the prominent ventral production of the thin-walled oral cup, which also extends as far backward as the posteroventral plane of the eye. The face and front are relatively narrow. The front at the vertex is about 3 times as wide as the ocellar triangle and at the antenna the face is scarcely twice as wide as the vertex. The ocellar tubercle is small but high and prominent, higher than the ocelli, an equilateral triangle in shape and set well forward from the rounded posterior corners of the eye. The antennae are widely separated, divergent, and set distant from the eye margin by no more than the width of the second antennal segment. The oral cup is large and quite elongate, very deep, with thin walls posteriorly which are vertical and are distinctly thickened on the anterior half of the recess and likewise narrowed anteriorly. The gena is quite linear and there is a tiny tentorial fissurelike tip. Viewed from above the occipital lobes have a horizontal fissure rather than a vertical one.

Thorax: The mesonotum is distinctly wider posteriorly, shining black, with slender, short, flat-appressed, scanty pile over much of the disc, and also

some scattered, erect, exceptionally fine, slender hairs. There are tufts of rather dense, erect bristly hair between the humerus and the wing. The notopleuron has 2 long, rather stout, curved, attenuate, sharp-pointed bristles. There are 3 bristles which are more slender above the wing and three, strikingly long, slender, black bristles along the postalar callosity, which are curved backward. Anterior mesonotal collar composed of a band of quite stiff, blunt-tipped, reddish-golden pile, continued across the front of the anterolaterally swollen humerus, and with a similar tuft directed upward from the dorsal half of the mesopleuron. Scutellum polished bluish black with long, very fine, erect hairs on the disc and longer slender bristles on the margin. The posteroventral mesopleuron, the upper sternopleuron, and the whole pteropleuron have scattered, fine, long, black, bristly hairs. Metapleuron with a vertical fringe of bristly pile and likewise some in front on the dorsal part. Hypopleuron entirely bare and no pile beneath the haltere. The plumula consists of coarse, long, white pile.

Legs: All of the femora are comparatively stout and the last four tibiae and tarsi likewise stout. However, the anterior tibiae and tarsi are very slender, completely smooth above; the tarsi reduced in size and bears fine, erect, nonglandular hairs. The anterior tibiae posteroventrally has an extremely dense, almost comblike band of short, stout setae. Middle femur with 1 or 2 bristles in front. Hind femur with at least 4 rather stout, long bristles on the ventral aspect of the distal half and 2 subapical bristles dorsally. Middle tibia with 5 to 7 weak, slender bristles in each row. Hind tibia with longer, slightly more stout bristles that are oblique. There are 4 anteroventrally, 6 anterodorsally, about the same number posterodorsally, and about 5 posteroventrally. All the femora are covered with flat-appressed, shining, black scales and some appressed setae. Claws very slightly curved, but curved backward, slender even at the base, and at most with minute stublike pulvilli.

Wings: Extraordinarily large, broad, blunt at apex, strongly narrowed at the base. The alula is wanting or at most quite linear and the axillary lobe greatly reduced throughout and attenuate basally. The entire wing is uniformly rather dark, sepia brown with a violet reflection above and below. There are 2 submarginal cells. There is sometimes a spur at the base of the second submarginal cell. The discal cell is very long and slender, and posteriorly the second submarginal cell is extended backward toward the wing base leaving the apex of the discal cell narrowed and pointed and the upper intercalary vein sigmoid. From the base of the second posterior cell there is a rectangular bend with a spur vein along the lower edge of the discal cell. Moreover, the discal cell lacks contact with the fourth posterior cell, and the posterior crossvein is generally present. The anal cell is widely open, the ambient vein complete. The costal comb is weak, but the basal spur is quite sharp and thornlike.

Abdomen: Abdomen elongate, and at the base barely or sometimes not quite as wide as the thorax. The abdomen is slightly narrowed posteriorly. The sides are nearly plane in both sexes to the end of the fifth segment, and the abdomen is at least $2\frac{1}{2}$ times as long as wide in males, a trifle shorter in females. There are 7 tergites visible. In the female the seventh tergite is large, triangular. The abdomen is shining, bluish black in color, the blue reflection strong. The pile consists entirely of sparse, scattered, exceptionally fine, erect, black hairs of moderate length, and along the sides of the tergites, in addition to the longer hairs. They are particularly dense along the sides and apex of the last tergite. Female terminalia with a row of nine, rather long, blunt-tipped, black-tipped, slender, golden-red spines on each acanthophorite. Male terminalia small, asymmetrical, more or less recessed. Male individuals smaller than females.

The male terminalia from dorsal aspect, epandrium removed, show a triangular structure. The epiphallus is more narrow than usual but still the basal part of the aedeagus is extraordinarily large and prominent, bulblike-shaped at the apex, and the dististyle is small, arising subapically from the basistyle and with an apical hooklike process and incision as seems to be typical of the subfamily. From the dorsal aspect the dististyle is elongate and slender. From the lateral aspect, the basistyle is quite long; the dististyle shows the characteristic incision, the epandrium is triangular with rather sharp basiventral lobe.

Material available for study: A series of the type-species collected by the author and his daughter in Mexico in 1951 and by the author and his late wife in Mexico in 1962. I have seen a second species.

Immature stages: Unknown.

Ecology and behavior of adults: I have captured individuals of both sexes hovering about and alighting upon shrubbery in Tepotzlan, Mexico. The locale was close to the borders of a mountain stream.

Distribution: Neotropical: *Cyananthrax cyanopterus* (Wiedemann), 1830 (as *Anthrax*).

Genus *Deusopora* Hull

FIGURES 173, 277, 664

Deusopora Hull, Journ. Georgia Ent. Soc., vol. 6, no. 1, pp. 1-3, 1971. Type of genus: *Deusopora sapphirina* Hull, by original designation.

Medium-sized flies, recognized by the large, very broad base of the wings, the triangular scutellum, and the peculiar color pattern. The basal two-thirds of the wings in both sexes is sepia brown with a strong violaceous reflection, the outer third water-clear and sharply demarcated. The venation is more like *Rhynchanthrax* Painter, the projection of the face and the antenna more like *Thyridanthrax* Osten Sacken. The humeral cell is slightly widened but the setae

brush narrow and instead of a curved spine, there is a broadly widened hook as in *Rhynchanthrax* Painter. The alula is narrow, the anal cell exceptionally widely opened. Mesopleuron with an anterior tuft and propleuron with a collar of orange pile. Abdomen elongate, rather narrow, shining black with emerald green scales and appressed, short, black, bristly or setate pile. All claws small but of nearly equal size.

This peculiar fly from southern Brazil is so aberrant and so unlike other members of the tribe *Villini* that I find it necessary to place it in a separate genus.

Length: 10 mm., wing 10 mm., base of wing 4 mm.

Head, lateral aspect: Head hemiglobular. The occiput is moderately prominent above, but shorter at the bottom of the head. The pile is flattened, brassy yellow, curled, and appressed flat. The central fringe is dense and short. The eye is large, rather long horizontally, with angulate, shallow, but extensive depression posteriorly, which extends from near the top of the eye to near the bottom. The eye is extensively bisected at the bottom of the indentation. The front is barely visible in profile, slightly more so on the lower half, with a shallow depression midway between ocellus and antenna, the pile erect and bristly. There are also some scattered, metallic-green scales on the front. The face is triangularly produced though not extensively produced. Medioapically the face, over a narrow, small space, is bluntly obtuse. Sides of face with a few pale scales and some appressed black setae and the anterior fifth of the oral cup bears a dense fringe of stout, black bristly setae overhanging the edge. A bare diagonal line goes from the eye margin to each antenna. Proboscis and labium distinctly shorter than the oral recess. The proboscis is rather stout, the labium thick. The palpus is long and cylindrical with a few fine, long hairs laterally and ventrally. It is more than half as long as the proboscis, labium excluded. The antennae are attached a little above the middle of the head, small, divergent, the first segment expanded medioapically and bearing moderately long setae on all sides including below. The second segment is distinctly shorter than wide, broadly attached to the third segment. The third segment is short conical and reaches almost maximum attenuation at the middle of the segment. Whole segment scarcely longer than the first two segments. There is a minute spine at the tip.

Head, anterior aspect: Wider than the thorax, circular, the vertex narrowly separated, almost equally narrow in both sexes. In the male the ocelli rest on the eye margin, and in the females it is separated from the eye margin by not more than the thickness of a posterior ocellus. The lower eye facets are pilose. The front at antenna is about 4 or 5 times as wide as at vertex. The antennae are widely separated and distant from the eye margin by the length of the first segment. The oral recess is long and slender, a little compressed anteriorly at the bottom of the eye, deep posteriorly, and extending quite back to the posterior plane of the eye. The genal suture along the anterior half of the

oral cup is quite linear, the fissure itself threadlike. The oral cup is slightly produced below the eye. From above, the lobes of the occiput, though prominent and more or less horizontal, are distinctly separated with a considerable gap between them. The ocellar tubercle is placed at the point where the corners of the eye are rounded backward and outward.

Thorax: A little longer than wide with parallel sides, except for the postalar callosity. The humerus is not greatly protuberant, and the posterior edge and surface are rounded. Mesonotum black with thin, grayish-brown pollen and with numerous, metallic, malachite-green scales, which are violet, placed over each wing. There is also some minute, fine, short, suberect hair, a few longer hairs in front of the scutellum. Anterior collar narrow, rather long, the coarse pile sharp apically, and bright yellow, and covering the anterior part of the humerus. Scutellum clothed with green scales like the mesonotum, with brown pollen and a few fine, long hairs on the margin. Propleuron with tufts of long yellow pile. Upper anterior mesopleuron with tuft of long, yellow pile. Whole posterior half of mesopleuron and upper sternopleuron with silvery white pile. The pteropleuron has some scattered dark hairs, and similar dark reddish-brown hairs are abundant on the upper half of the metapleuron. The entire hypopleuron is bare and there is a tuft of pile beneath the haltere.

Legs: Moderately well developed, the front pair is scarcely reduced, the anterior femur and tibia are smooth. Middle femur without spines or bristles anteriorly and no ventral hair. Hind femur likewise without spines or fringe of hair below. All these femora are covered with dark, flat-appressed, shining, slender scales, and with a few very minute, appressed, fine, setae dorsally and laterally along the hind femur. Hind tibia with 5 or 6 fine, oblique, short, stiff, bristly hairs ventrolaterally. Dorsally, on both sides, the hind tibia has 20 or more short, somewhat more stout, oblique, spiculate setae. Anterior claws a little reduced, but no more than the posterior claws which are very small, sharp, scarcely curved, with no pulvilli.

Wings: Extraordinarily broad, a little less than twice as long as the maximum breadth. The wings are dark, sepia brown with strong violet to greenish reflection, this dark color is vertically delimited very close to the outer end of the discal cell. There are 2 submarginal cells. The second vein arises obliquely, distant from the anterior crossvein, by more than half the length of that crossvein. First posterior cell open maximally. Second posterior cell quite small, narrowed basally. Contact of the discal cell with the fourth posterior cell as long as the anterior crossvein. This crossvein enters the middle of the discal cell. Anal cell very widely open by a length two-thirds the length of the anterior crossvein. Second anal vein straight. Axillary lobe broad. Alula 2 or 3 times as long as wide.

Abdomen: Elongate oval, no wider than the thorax, with almost parallel sides for the first 4 or 5 tergites.

The length of the abdomen is $1\frac{1}{2}$ to 2 times the length of the mesonotum, the scutellum excepted. The abdomen is shining black, rather densely covered with brilliant green, flat-appressed scales. The lateral sixth of the first tergite and anterior corners of the second have erect, coarse, moderately dense reddish-brown pile; the curled-over margins of the tergite and the last three tergites posteriorly have a few fine, black, appressed hairs. Eight tergites are visible from above. The eighth tergite is large, triangular, sloping or compressed downward or inward at the end of which the terminalia bear 6 pairs of black spines and laterally a tuft of fine yellow hair. These appear to be rather commonly exposed in the female by a beaklike gape of the last sternite. Male terminalia asymmetrical, small, and recessed.

Material available for study: The type series.

Immature stages: Unknown.

Ecology and behavior of adults: Unknown.

Distribution: Neotropical: *Deusopora sapphirina* Hull.

Genus *Dipalta* Osten Sacken

FIGURES 186, 370, 662, 665, 944, 945

Dipalta Osten Sacken, Bull. U. S. Geol. Survey, vol. 3, p. 236, 1877. Type of genus: *Dipalta serpentina* Osten Sacken, 1877, by monotypy.

Flies of medium size with conical face and 3 submarginal cells which are rather readily recognized by the mottled wings and the erratic venation. As Osten Sacken pointed out the second vein is greatly contorted, bent into the form of a recumbent S-like figure situated near the point of contact with the anterior branch of the third vein; however, the exact shape of this vein is very variable and generally there are one or more spur veins directed either backward or outward; however, spur veins may be absent.

The genus is related to the *Villa* Lioy complex rather than to *Exoprosopa* Macquart from which it is easily separated by the absence of the terminal stylelike segment attached to the third segment. It is most closely related to *Diplocampta* Schiner. Like that genus it has 3 submarginal cells, but the wing base in *Diplocampta* is very narrow, the bend in the third vein, anterior branch, very deeply kinked and sigmoid.

Dipalta Osten Sacken is known from one species ranging over northern Mexico and the western United States and one species from Virginia and Ohio. It is quite possible that there is only a single highly variable species among which a number of subspecies may be distinguished. I have collected it from nine localities in seven states including three from Mexico.

Length: 9 to 10 mm.; wing 10 to 13 mm.

Head, lateral aspect: The head is hemiglobular and rather triangular in shape because of the strongly peaked or conical and triangular face. The occiput is

extensive, especially on the upper part of the head. At the bottom of head, it is comparatively short. The pile is scanty, scalliform, and completely flat-appressed; the central fringe around the recess is dense, but short. The front is very slightly raised above the eye margin, flat across the middle, or even slightly depressed. Its pile is erect, not longer than the first antennal segment, abundant without being dense, and extending from vertex to the base of the antenna. In addition there are numerous, slender, flat-appressed scales on the front; the vertex, however, is pollinose only in addition to the hair. Face produced forward as an almost equilateral triangle. Its pile consists of scanty, scattered, short, subappressed hairs, a fringe of somewhat stiffer, more bristly hairs in the middle along the edge of the oral cup, and also numerous appressed scales like those of the front. There is also a narrow, scarlike, bare band or creaselike band, extending from near the middle of the oral recess laterally around to the base of each antenna. The eye is large, upper facets small, anterior facets enlarged somewhat in the middle of the eye. There is a deep, but very broad or extensive indentation, and a bisecting line at the middle of the eye posteriorly which extends a short distance forward. The eyes have a strong, greenish reflection.

The proboscis is short, rather slender, a little flattened, grooved laterally, and not extending beyond the oral recess. The labellum is rather long, slender, and flattened. The palpus is long and filiform with a few, fine, erect hairs laterally. The antennae are attached at the upper third of the head and are comparatively small. The first segment is twice as long as its basal width, but it is a little widened apically, and there are some short setae dorsally, slightly longer setae laterally. Second segment narrow at the base, rather rounded and beadlike, and not as long as wide. The third segment forms a short, bulblike base, triangular outwardly; it is slightly wider than the second segment and has a short, abruptly formed, slightly attenuate style, carrying a minute spine at the tip.

Head, anterior aspect: The head is not quite as wide as the posterior mesonotum. It is nearly circular from the front. The eyes in the male are separated by about twice the width of the ocellar tubercle. Ocellar tubercles are strongly and abruptly raised and set distinctly forward from the posterior eye corners, and the ocelli occupy an equilateral triangle. The posterior eye corners are only slightly rounded. The antennae are comparatively widely separated, but are distant from the eye margin by the length of the first antennal segment. The oral opening is long, large, quite deep, with vertical sides in the middle, overhanging edges posteriorly. The margin is paper-thin posteriorly, a little thickened on the anterior half. Gena linear. Tentorial pits absent. Viewed from above, the lobes of the occiput have a vertical fissure.

Thorax: The mesonotum is distinctly widened posteriorly but the humerus is prominent, vertically truncate posteriorly, and extends outward considerably, and

the dense, stiff, erect hair of the anterior collar extends over the humerus in full. Prosternum with long tufts of equally stiff and bristly hair. The mesonotum is more or less opaque black, generally with dark brown pollen and loosely covered with flat-appressed, short, pale, slightly scaliform hair, which extends also over the whole scutellum, but both areas are apt to be largely denuded. The notopleuron has several long, slender bristles and others extend up to the base of the humerus. Postalar callosity with long slender bristles. The margin of the scutellum may have 4 or 5 pairs of still more slender bristles. Upper half of mesopleuron with numerous, long, stiff or bristly hairs, pale in color, extending outwardly and upwardly. Remainder of mesopleuron with more slender or shorter pile appressed backward or downward. The pteropleuron has an anterior tuft of stiff pile. The whole of the metapleuron is covered with long, stiff hairs, and there is an anterior and posterior tuft of appressed, stiff hair beneath the haltere. Hypopleuron bare, front and behind. Squama with a very short fringe of scales.

Legs: Comparatively strong without being stout or swollen. Anterior and middle femur, slightly narrowed apically. The middle femur has 2 or 3 rather strong bristles anteroventrally at the middle. Hind femur with 5 or 6 more slender, short bristles along the posteroventral margin; however, the last one distally is a little more stout. Anterior tibia slender and characteristically quite smooth without bristles or spicules. Anterior tarsi reduced in length, and the whole of the anterior pair of legs somewhat reduced in size. Anterior tarsus bears vertical, glandular-tipped hairs vertically. Middle tibia with some quite fine, short, slender bristles, 7 or 8 anterodorsally, the same number posterodorsally and posteroventrally, but only 4 or 5 anteroventrally. Hind tibia long, with 15 or more bristles in the anterodorsal row. There are about 10 in the posterodorsal row, 7 or 8 in the posteroventral row, but only 5 or 6 anteroventrally; all these bristles are only slightly stronger than those of the tibia. The hind femur may bear 7 or 8 oblique spicules of bristles dorsally at the middle and on the outer half. Claws sharp, curved from the base, without pulvilli.

Wings: The wings are large and elongate, characteristically mottled with comparatively sharp, dark brown spots and irregular brown group of coalesced spots crossing the wing at the middle where the second vein arises. A still more irregular wide group of coalesced spots are located subapically on the outer third of the wing. The venation is quite erratic especially with regard to the second vein, and to a less extent with the third vein. The second vein arises abruptly near or very close to the anterior crossvein, but makes a rounded bend outwardly. There is a deep loop at the end of the marginal cell, sometimes with a spur outward from this loop, and there is a second broad loop forward, located in front of the base of the second submarginal cell, of very variable shape and sometimes with a backward spur. There are 3 submar-

ginal cells formed, as I interpret it, by the posterior branch of the second vein, going backward to join the anterior branch of the third vein. This seems to me a logical interpretation of this wing. Base of the second submarginal cell sometimes with a backward spur. Contact of the discal cell with the fourth posterior cell comparatively short. Anal cell open, usually widely. Axillary lobe long and narrow. Alula present with circular posterior margin. Ambient vein complete. Costal comb large, the setae minute, the basal spur sharp and thornlike.

Abdomen: The abdomen is as broad as the thorax, slightly elongate in most forms. The abdomen is usually a dully shining black color, in some forms yellowish along the sides. The whole surface is rather abundantly covered with short, flat-appressed, yellow, scaliform pile with a little black hair in the middle. In addition, there is generally a loosely formed, very fine, obliquely erect band of fine, black, bristly hairs of no great length along the posterior margin of the tergites. Normally 7 tergites are visible. Occasionally, the eighth and ninth can be seen, very small and short. Male terminalia asymmetrical, more or less recessed and of no great size.

The male terminalia from dorsal aspect, epandrium removed, show a figure very broad on the basal half and the epiphallus very large, wide apically, with rounded, tongue-like structure. From the lateral aspect the small, rather elongate, slender dististyle is incised apically with upturned hook. The epandrium is rectangular with a rather prominent, downturned lobe basally.

Material available for study: A considerable series collected by Marguerite Hull and me in Western States and in Mexico. Several new species may be involved. What bee flies may parasitize the giant *Palpares* in South Africa?

Immature stages: Flies of this genus parasitize ant-ions (Myrmeleonidae).

Ecology and behavior of adults: I have found these flies comparatively abundant on low-growing flowers in desert areas. I have no record of the plants, but they were found frequently on a greenish-yellow flower in the Ruidoso Mountains of New Mexico.

Distribution: Nearctic: *Dipalta banksi* Johnson, 1921; *serpentina* Osten Sacken, 1877.

Genus *Diplocampta* Schiner

FIGURES 195, 391, 671, 674

Diplocampta Schiner, Verh. zool.-bot. Ges. Wien, vol. 17, p. 312, 1867. Type of genus: *Diplocampta singularis* Schiner, 1868, by original designation.

Curran (1931), pp. 7-8, key to 3 West Indian and Neotropical species.

Small flies of *Villa*-like aspect, with 3 submarginal cells, but at once distinguished by the characteristic S-shaped bends in the anterior branch of the third vein

and apical part of second vein. Moreover, the wing is strongly narrowed toward the base, with widely open anal cell, which together with the scales on face and abdomen, the small size, etc., relate them to *Mancia* Coquillett which shares these peculiarities, except that its venation is normal. The face of *Diplocampt* Schiner is moderately produced but blunt and for a portion of its height nearly vertically plane. Anterior tibia without spicules. These flies do not appear to be closely related to *Neodiplocampt* Curran, which, instead of an onion-shaped third antennal segment, has a long conical one, has 2 submarginal cells and only gently sigmoid radial veins, and is besides larger, with the wing normally wide at base and scales rather more poorly developed.

This small genus is known only from southern South America.

Length: 4 to 6 mm.

Head, lateral aspect: The head is subglobular, the face prominent but blunt anteriorly, hence there is no conical peak. The face is covered loosely with beautiful broad, oval, rather pale scales, together with loosely scattered, not very long, erect, or subappressed, black, bristly hairs. The front has the same kind of covering of scales and hairs, the bristly pile somewhat more erect, especially on the upper half of the front where it is also somewhat longer. The occiput is comparatively short, with large, central cavity that has a dense fringe of short, erect pile along its margin. Lateral portion of occiput conspicuously but loosely covered with short, pale scales. Occiput bilobate above with deep medial fissure. Posterior eye margin very shallowly indented but obtusely angular in the middle with short, medial notch. The eye is almost as long as high. Palpus long and slender, curled upward with long, scattered, very fine hairs ventrally. Proboscis short, not extending beyond the oral opening. The antenna is attached at the upper third of the head and all 3 segments quite short. The first segment is a little longer than the second; it bears numerous, short, erect, black setae laterally and also medially. The second segment is 2 or 3 times wider than long, third segment wider than the second at the rimlike base which is no longer than the second segment and then abruptly expands into a long, stylelike process of approximately 2 or more times the length of the basal, bulbous part. Apex with a minute spine and possibly 1 or 2 very minute microsegments.

Head, anterior aspect: The head is distinctly wider than the thorax, the vertex of the female is narrow, about one-third as wide at the front as the antenna. The antennae are widely separated, each is separated from the eye margin by a little less than the width of the first segment. Ocellar tubercle low, of an equilateral triangular shape and with vertical sides.

Thorax: The thorax is short, the mesonotum dully shining black, very slightly convex and rather loosely covered with narrow scales which may be brownish in

the middle and white anteriorly. Anterior margin with a narrow collar of erect, not very long, coarse pile. The protuberant humerus bears long, coarse hairs and similar scaliform pile which is continued down over the notopleuron. The notopleuron has 3 delicate, slender, black bristles. The postalar callosity has 2 or 3 longer, somewhat stouter, sometimes reddish bristles. Margin of the scutellum with 3 or 4 pairs of longer, slender bristles which are black or sometimes yellow, the inner pair crossed. Squama with a fringe of slender scales. Mesopleuron with scanty, loosely scattered, long, bristly hairs curled upward along the dorsal border, and a few appressed scaliform hairs postero-ventrally. Pteropleuron likewise with a few long bristles or bristly hairs curled backward. Metapleuron with a vertical posterior band of long, fine, erect pile. Hypopleuron bare.

Legs: The legs are slender, short, and delicate. The femora and tibiae bear rather dense, matted, pale, glistening scales. Middle femur with a fringe of loose pile posteriorly. Anterior tibia without spicules of any kind, but middle and hind tibia with well-developed spicules though unusually slender and of no great length; these are situated in 4 rows containing from 7 to 16 elements. Claws exceptionally slender, pulvilli absent.

Wings: The wings are characteristically narrowed toward the base and a little broadened and rounded apically at least by contrast with the base. The shape is much as found in *Mancia* Coquillett. The apex of the wing is sometimes tinged with brown, otherwise hyaline. The venation is characteristic, the second vein arises at or barely before the anterior crossvein; it is rectangular with basal spur. The second vein beyond the fork on its anterior branch is remarkably sigmoid and contorted, quite S-shaped. The anterior branch of the third vein forms a short, plane, rectangular crossvein. Anal cell widely open, alula short, base of the costa with a small, flangelike expansion and comb, the basal lobe spinelike. The proximal vein at the base of the third posterior cell has an inward spur into the discal cell.

Abdomen: The abdomen is about $1\frac{1}{2}$ times as long as the thorax and not any wider at the base. From the base it is gently and regularly narrowed and rounded at the apex. Surface covered with rather dense, flat-appressed, pale scales often of two or more colors. Posterior margin of the first tergite with a conspicuous row of radiating scales and on the anterior half with a few fine, scattered, erect hairs changing in the antero-lateral corners to dense, coarse, short pile. Posterior margin of the tergites also with a scanty fringe of more or less appressed, very fine, slender, black, bristly hairs. Sternites similar to the tergites.

Material studied: Examples in the collection of the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical: *Diplocampta secunda* Paramonov, 1931; *singularis* Schiner, 1868; *subsiniata* Oldroyd, 1938.

Genus *Hemipenthes* Loew

FIGURES 177, 178, 183, 185, 187, 413, 672, 678, 942, 943

Hemipenthes Loew, Berliner Ent. Zeitschr., vol. 13, p. 28, nota 1869. Type of genus: *Musca morio* Linné, 1758. Designated by Coquillett, p. 550, 1910; two species as one.

Isopenthes Osten Sacken, Biologia Centrali-Americana, Dipt., vol. 1, pp. 80, 96, 1886. Type of genus: *Anthrax sinuosa* Wiedemann, 1821, as *Isopenthes jaccnickeana* Osten Sacken, 1886, subspecies. Designated by Coquillett, p. 556, 1910, the second of two species.

Engel (1936), pp. 563-564, key to 7 Palaearctic species.

Painter (1962), pp. 80-90, key to 12 species from the United States.

Small to rather large flies with the basal half, and sometimes more than half or even the whole wing, dark sepia brown or blackish; the blackish color is sharply defined, diagonal or oblique, either with irregular, steplike edge or smooth, and often extending no farther backward than the end of the second submarginal cell. The face is either rounded and retreating, or at most blunt and vertical, apt to be rather heavily covered, together with the front, with erect stiff pile. The third antennal segment is onion-shaped at base, rather abruptly narrowed with long, fine style as in *Rhynchanthrax* Painter, but never so strongly reduced to a bulb-like base. Anterior tibia smooth, without spinules or at most fine, sharp, small ones scarcely noticeable. The flies of this genus, as Bezzi has pointed out are rather readily distinguished from *Villa* Loey by the wide, obtuse ending of the discal cell compared with the acute apex in *Villa* Loey. Bezzi calls attention to the small costal comb in comparison with *Villa* Loey; he calls the metapleural fringe sparse, and this may be true of some European species, but I do not find it so in my material.

Hemipenthes Loew is abundant in the Palaearctic and Nearctic regions, less so elsewhere and apparently absent from South Africa.

Length: 5 to 14 mm.

Head, lateral aspect: The head is hemiglobular, the occiput moderately developed, a little shorter below and the pile of the occiput is fine and appressed forward toward the eye and in one species before me, from Mongolia, some of the short setate hair is nearly erect. In some species it is nearly scaliform. The eye is reniform, the facets of nearly equal size, the posterior indentation is shallow, but quite broad, extending some distance above and below the middle of the eye. The eye is distinctly bisected by a line extending a considerable distance inward over the eye from the midpoint of the excavation. The front is comparatively wide, covered with dense, conspicuous, erect, black, bristly pile and a few small, short appressed scales in some species. These scales are virtually lacking in some species.

The face varies from quite bluntly protuberant, nearly or quite vertical beneath the antenna, to others in which it is even rounded and retreating. The face is covered with similar, dense, bristly pile and scales like that of the front, and this bristly pile forms a distinct fringe, extending over the margin of the oral cup on the anterior half of the cup. The proboscis is short characteristically, varying from species where it extends just to the apex of the oral recess to others in which it is scarcely more than half as long as the oral recess. This marked reduction in the length of the proboscis is perhaps a trend in the same direction as such species as *Anthrax* Scopoli and *Oestranthrax* Bezzi. The proboscis is quite stout and the labellum large and fleshy as in a muscoid. Palpus slender, cylindrical or filiform, often curled or coiled, and with a fringe of fine hairs ventrally and laterally. Sometimes the labellum though large is elongate oval and flattened. The antennae are attached at the middle of the head and are comparatively small and short. The first segment is about twice as long as wide, a little widened apically or extended medioapically and bears especially on the outer half numerous, moderately long, stiff, bristly hairs, never quite as long as the segment itself. They may extend almost to the base. The second segment is short and beadlike, rounded in the middle, and narrowly attached to the third segment. The third segment is as wide as, or very slightly wider than, the second segment, bulbiform, onion-shaped, or very short conical, to which is attached a rather slender style. The style is approximately as long as the first two antennal segments or very slightly longer, and it bears a minute spine at the apex.

Head, anterior aspect: The head is approximately the same width as the mesonotum between the wings. It is nearly circular from the anterior view, or may be very slightly flattened on all four sides. The eyes are narrowly separated in the male by a distance approximately equal to the length of the first anterior segment. They are a little more widely separated in the female. The ocellar tubercle is nearly equilateral, has vertical sides, is almost hidden by the overgrowth of the eye on each side. The antennae are less widely separated than in some related genera, the distance between the antennae being little more than one-third the width of the front at this point. The oral cup is rather wide, about $2\frac{1}{2}$ times as long as its width. It is deep anteriorly and especially posteriorly. In some species the sides are quite wide anteriorly, in others narrow and sloping. The gena is rather narrow but the tentorial fissure is deep midway between the antenna and the posterior end of the recess. This fissure is conspicuously deep. Viewed from above the lobes of the occiput are swollen posterodorsally and consequently the fissure is more or less horizontal with a pitlike depression behind the ocellar column.

Thorax: Wider posteriorly, blackish in color with loosely scattered, fine, appressed hair or scaliform pile. The humerus is rather strongly swollen out laterally and the wide anterior collar of stiff pile extends over

and includes the whole of the humerus. In both American species and species from Central Asia there is often a dense, lateral band of appressed pale pile running down the sides of the mesonotum and extending over at least part of the postalar callosity. In some species there is additional pile on the disc of the mesonotum, consisting of exceptionally fine, erect hairs. Notopleuron with a few bristles and sometimes they may be quite stout. Similarly there may be several long stout bristles on the postalar callosity and some bristles, either fine or stout, on the margin of the scutellum. The disc of the scutellum, unless denuded, is covered very much like the mesonotum. The pleuron is rather densely pilose, with dense, coarse tufts on the propleuron, most of the sternopleuron, whole of the mesopleuron and meta-pleuron, and most of the pteropleuron. The hypopleuron is bare above the middle coxa. There is a little pile above the posterior coxa and a distinct short, appressed tuft of pile beneath the haltere. Squamal scales short.

Legs: Comparatively stout, but not swollen. Anterior femur with a fringe of stiff hairs ventrally on both sides in some species. The anterior tarsi are nearly smooth in some species but may have a few oblique slender setae or bristly hairs dorsally. Middle femur with stiff hairs beneath in some species, hind femur similar but may have 3 or 4 long slender bristles antero-ventrally of varying proportions, rather short in some species. Basal half of hind femur with some long, fine, stiff hairs ventrally. All the femora and tibiae have some scales which may be conspicuous and long in some species, especially where they are pale in color. Middle tibia with a few, fine, oblique bristles. Hind tibia with slightly stronger bristles in 4 rows. Including small elements there are 15 to 25 bristles and spiculate setae in the anterodorsal row, and 10 to 15 in the postero-dorsal row. There are 5 to 7 in each ventral row. In at least one species the hind tibia is a little flattened and strongly feathered above and below with conspicuous blackish scales. The tarsi are slender and attenuate posteriorly. Claws small, sharp, nearly straight, with small pulvilli. Anterior claws very minute.

Wings: Comparatively uniform in width. The wings are wide apically and basally with a characteristic black or reddish-brown pattern, obliquely, but irregularly and sharply distributed on the basal half of the wing. Sometimes this dark pattern leaves as much as half of the anal cell and axillary lobe clear and sometimes with this area almost entirely blackish and with the dark color sometimes ending at or even before the middle of the wing and in others more or less filling completely the marginal cell and beyond. There are only 2 submarginal cells. The second vein arises abruptly at just before or just beyond the anterior crossvein. Marginal cell generally bent backward like a thumb at the apex. Usually there are some faint spots about the crossveins within the dark basal portion of the wing. The anterior crossvein enters the middle of the discal cell. The upper anterior intercalary vein may be oblique or

rectangular, and apically the discal cell may be relatively narrow or may be widened above and below. Contact of discal cell with the fourth posterior cell usually not longer than the length of the anterior crossvein. Anal cell widely open. Alula narrow. Ambient vein complete. Costal comb weak and narrow. The costal hook sharp and thornlike.

Abdomen: Short oval, sometimes no wider than the thorax, again distinctly wider though not greatly. The color is black. There are 7 tergites, which are clothed with moderately dense hair either appressed or sub-appressed, fine and curly, or matted and scaly, black, whitish, yellow or brownish orange in color, and often mixed. Sides of the tergites with a rather inconspicuous fringe of coarse hair and sometimes larger tufts. In some species the dense lateral fringe of the first tergite extends entirely down the sides of the second tergite, and there may be alternating tufts of black and pale pile. Females with a few slender bristly spines along the acanthophorites. Male terminalia small, conical and asymmetrical, partly exerted beneath the last tergite. The remaining tergites beyond the seventh are completely tucked in under the seventh.

The male terminalia from dorsal aspect, epandrium removed, show a basally wide, apically narrowed figure with broad, long, spatulate or tongue-like epiphallus with concave sides, very blunt at apex and the dististyli are nearly apical, as they arise from the basistylus. Basal part of the aedeagus large, very short oval, and rounded both basally and apically. From the lateral aspect the epiphallus has a ventral extension in the middle, the dististylus is comparatively short, basistylus long and the epandrium has a wide, archlike or concave incision ventrally from the anterior to the posterior corners.

Material available for study: In addition to the series at several museums, I have material sent me by the late Dr. Timon-David and also considerable material collected by myself and my late wife in the western United States.

Immature stages: The larvae of *Hemipenthes* Loew behave as hyperparasites of parasitic Hymenoptera such as the genera *Banchus* and *Ophion* and also hyperparasites of such tachinids as *Masicera* Macquart, which in turn have attacked nocturnal *Lepidoptera*.

Ecology and behavior of adults: Species of this genus are abundant on various types of flowers, mostly composites.

Distribution: Nearctic: *Hemipenthes bigradata* (Loew), 1869 (as *Anthrax*); *castanipes* Bigot, 1892; *catulina* (Coquillett), 1894 (as *Anthrax*); *celeris* (Wiedemann), 1828 (as *Anthrax*) [= *floridensis* Macquart, 1849]; *chimaera* (Osten Sacken), 1887 (as *Anthrax*); *comanche* Painter, 1962; *curta* (Loew), 1869 (as *Anthrax*); *edwardsii* (Coquillett), 1894 (as *Anthrax*); *eumenes* (Osten Sacken), 1887 (as *Anthrax*); *floridana* (Macquart), 1850 (as *Anthrax*); *incisiva* Painter, 1962 [= *incisa* (Walker), 1852 (as *Anthrax*)]; *inops* (Coquillett), 1887 (as *Anthrax*);

lepidota (Osten Sacken), 1887 (as *Anthrax*); *mobile* (Coquillett), 1894 (as *Anthrax*); *morio* (Linnaeus), 1758 (as *Musca*) [= *morioides* (Say), 1823 (as *Anthrax*)]; *pima* Painter, 1962; *pullata* (Coquillett), 1894 (as *Anthrax*); *sagata* (Loew), 1869 (as *Anthrax*) [= *orbitalis* (Williston), 1901 (as *Anthrax*)]; *scylla* (Osten Sacken), 1887 (as *Anthrax*); [= *succincta* (Coquillett), 1894 (as *Argyromoeba*)]; *seminigra* Loew, 1869; *sinuosa* (Wiedemann), 1821 (as *Anthrax*) [= *assimilis* (Macquart), 1846 (as *Anthrax*)], = *concosa* (Macquart), 1840 (as *Anthrax*), = *gideon*, authors, not Fabricius, = *nycthemerus* (Macquart), 1840 (as *Anthrax*); *sinuosa blanchardiana* (Jaenicke), 1867 (as *Eroprosopa*), *sinuosa jaenickeana* (Osten Sacken), 1886 (as *Isopenthes*); *webberi* Johnson, 1919; *wilcoxi* Painter, 1933; *yagui* Painter, 1962.

Neotropical: *Hemipenthes minas* Macquart, 1848.

Palaeartic: *Hemipenthes alata* Becker, 1907; *argentifrons* Becker, 1907; *chorassani* Becker, 1913; *circumdata* Becker, 1912, *circumdata quinquefasciata*, Becker, 1912; *gaudania* Paramonov, 1927; *hamifera* (Loew), 1854 (as *Anthrax*); *intermedia* Paramonov, 1927; *latipennis* Paramonov, 1927; *maura* (Linné), 1758 (as *Musca*) [= *bifasciatus* (Meigen), 1804 (as *Anthrax*)], = *daemon* (Panzer), 1797 (as *Anthrax*), = *denigratus* (Linné), 1767 (as *Anthrax*), = *hirsutus* (Villers), 1789 (as *Anthrax*), *maura flavotomentosa* Paramonov, 1926; *melaena* Bowden, 1965; *mischanensis* Paramonov, 1926; *morio* (Linné), 1758 (as *Musca*) [= *morioides* Say, 1823, = *semiater* (Meigen), 1820 (as *Anthrax*), = *seminiger* (Loew), 1869]; *nitidofasciata* (Portschinsky), 1891 (as *Anthrax*); *praecisa* (Loew), 1869 (as *Anthrax*); *rufipes* Becker, 1912; *subarcuata* (Loew), 1870 (as *Anthrax*); *transaspica* Paramonov, 1926; *uncina* Loew, 1869; *velutina* (Meigen), 1820 (as *Anthrax*) [= *bicinctus* (Wiedemann in Meigen), 1820 (as *Anthrax*)], = *holosericeus* (Meigen, not Fabricius), 1804 (as *Anthrax*), = *nycthemerus* (Wiedemann in Meigen), 1820 (as *Anthrax*).

Genus *Lepidanthrax* Osten Sacken

FIGURES 211, 567, 702, 946, 947

Lepidanthrax Osten Sacken, Biologia Centrali-Americana, Dipt. vol. 1, p. 107, 1886. Type of genus: *Anthrax disjunctus* Wiedemann, 1830. Designated by Coquillett, p. 559, 1910, the first of 3 species.

Podolepidia, new subgenus. Type of subgenus: *Eroprosopa lutzi* Curran, 1930.

Curran (1930), pp. 1-2, key to 12 North American species.

A genus of comparatively small flies readily distinguished by the length of the slender proboscis which extends a considerable distance beyond the end of the oral recess and is nearly or sometimes quite twice the length of the head. Another important character concerns the antenna; the third segment is minute, abruptly onion-shaped, the style quite long, almost threadlike and without suture and ends in a minute,

short bristle at the apex; the antennae are unusually widely separated.

The front tibia bears distinct, slender spinulate bristles dorsally. There are no pulvilli. The wings are completely hyaline in some species with only the subcostal cell yellowish. In other species the costal cell is tinted and a small spot about the anterior crossvein, and in still others there is a dark brown costal cell and a distinct pattern of small, more or less isolated blackish spots. First posterior cell in some species with supernumerary crossvein near the end of the discal cell. Contact of discal cell with posterior cell unusually long. The tergites of the broad, short, rather flattened abdomen have numerous appressed scales, and the lateral margins have extending fringes of scales which are sometimes quite wide. These mats of scales are sometimes brilliantly silver or pale golden.

This group of flies is found widely in the southwestern United States and Mexico and ranging east to Texas and New Mexico and south to Panama. Two species from India have been assigned by Brunetti to this genus and two from Australia by Roberts; I have not seen these.

Length: Most species 5 to 9 mm., proboscis excluded; 1 species reaches 11 mm.

Head, lateral aspect: Head semiglobular, the occiput unusually prominent, especially in the middle on account of the long, quite deep, angular indentation of the eye. Eye sometimes with a short bisecting line, or sometimes only with the facets curving forward at the bottom of the indentation. The pile of the occiput is dense and composed of conspicuous, short, broad, flat-appressed scales; the posterior fringe around the central recess is rather long and dense. The front is flattened or in some species very slightly raised in front of the ocelli and flattened or even a little depressed on the lower half. Pile of the front and vertex, consisting of comparatively short, erect, fine hairs which are scanty and sparse, but stiff and bristly in the larger species. Characteristically the front is also covered densely with a conspicuous mat of broad, pale-colored, flat-appressed scales. The face is conically or triangularly extended forward conspicuously, extending well beyond the end of the third antennal segment if the style be excepted. Pile of face, like that of the front, with scattered, fine, bristly hairs and numerous broad, conspicuous, pale appressed scales.

The proboscis is long and slender, extending far beyond the oral recess. Its total length is about 1½ times the head length; the labellum is small and slender, and the surface microspinulose. Palpus long, slender, and filiform with fine, erect, stiffened, ventral hairs. The antennae are attached at the middle of the head. They are small, the first segment slightly longer than the second, both these segments a little widened apically. The third segment a little rounded at the base, the whole segment is small and more or less globular or bulblike, with an abruptly formed, long, slender,

filiform style, rather like that of *Stonyx* Osten Sacken. The style bears a minute spine at the apex.

Head, anterior aspect: The head is not quite as wide as the posterior width of the mesonotum. It is nearly circular, slightly flattened above, below, and laterally, the eyes in the male are separated by a little more than twice the width of the ocellar tubercle, a little more widely in females, and the entire face and front comparatively narrow. Upper eye facets small. Anterior eye facets opposite the antenna enlarged. The eyes often have a greenish tinge. They are large, high, and reniform. The antennae are quite widely separated from the eye margin by not more than the length of the first segment. The oral recess is quite long, slender, deep, with vertical sides, even anteriorly, the margin thin, the cavity a little wider posteriorly and the oral cup extending a little downward beneath the eye. The tentorial fissure is rather anterior to the middle of the recess, and the gena appears to be linear. There is a small bare triangle at the bottom of the posterior eye corner. The ventral eye corners are broadly rounded in some species, angular in others, but the vertical eye corners are broadly rounded in all species.

Thorax: Short, almost quadrate, a little wider posteriorly as in *Stonyx* Osten Sacken. The mesonotum is feebly shining with faint pollen, densely covered with appressed, slender scales, and the scutellum similarly covered. There may be a few long, slender, bristly hairs in front of the scutellum and in front of the wing. Notopleuron and postalar callosity with comparatively stout, moderately long bristles. Margin of the subtriangular scutellum with rather long, slender bristles. The anterior collar is rather extensive, comparatively long and stiff anteriorly, grading off into shorter pile posteriorly. Only the upper half of the mesopleuron has bristly pile. The lower half in most species has numerous, quite broad, conspicuous, pale scales, occasionally more slender in some species. Both pteropleuron and sternopleuron with patches of scales and some stiff hair. The pteropleuron may have hair only. Metapleuron with a conspicuous, vertical fringe of stiff, bristly hair. Posterior hypopleuron below the haltere with a patch of scales, and there is a tuft of hair immediately beneath the haltere, another one posterodorsally behind the spiracle. Haltere small with a small knob. Squamal fringe composed of slender scales.

Legs: Neither stout nor slender, the anterior femur a little thickened toward the base, and all the femora and tibiae densely covered with broad, short scales. Anterior femur sometimes with a row of long, stiff hairs ventrally, bristles absent. Middle femur with 2 to 4 stout bristles anteroventrally along the middle. Hind femur with 4 or 5 similar, slightly larger bristles along the anteroventral margin. Anterior tibia with 5 or 6 minute, fine bristly spicules on the anterodorsal segment and as many as 10 on the posterodorsal margin. Middle tibia with 5 to 7 stronger and longer bristles on the anterodorsal margin, 8 or 10 on the postero-

dorsal margin and 6 or 7 on the posteroventral margin and almost as many weaker bristles on the anteroventral margin, making 4 rows. Hind tibia similar, the bristles equally large but fewer in number. All of the tarsi are quite weak, poorly developed, short and slender and attenuate. Claws scarcely curved, pulvilli absent.

Wings: Characteristically slender, varying from hyaline with only the subcostal cell tinted yellow to species with 1 or 2 small brownish spots to species with numerous, sharply defined, brown spots. There are 2 submarginal cells. One group of species has an extra crossvein across the first posterior cell near the end of the discal cell. These are much larger than the usual *Lepidanthrax* and may be placed in the subgenus *Podolepida*, new subgenus, with *lutzi* Curran as type. The discal cell is in contact with the fourth posterior cell for a very considerable distance. The first posterior cell is a little narrowed apically. The anal cell is very widely open apically. Alula well developed. Ambient vein complete. The costal comb varies from small to wide and extensive. The costal hook is sharp and thornlike.

Abdomen: Wider than the thorax in most species, comparatively flattened. There are 7 tergites visible. In most species the abdomen is feebly shining black, but in some species the sides of the tergites, and as many as the last five tergites, are pale brownish yellow. Characteristically the pile of the abdomen consists of dense mats of scales, often silvery, which in a few species are confined to the lateral margins of the tergites. The last two tergites have the pile elsewhere consisting of flat-appressed, scaly hair. There is a difference between the sexes in some species. The males may have mats of silver scales on the terminal half of the abdomen, which are appressed in an outward direction laterally. Females of such species may have the silver scales replaced by oblique mats of slender, whitish scales. However, in addition to the scales and the appressed scaly hair, most species with a few exceptions have a single row of long, slender, blackish, bristly hairs along the posterior margin of the tergites. Sternites likewise covered with scales and with long, slender, erect, bristly hairs. Male terminalia comparatively small and recessed.

The male terminalia from dorsal and lateral aspect, epandrium removed, show a figure basally broad, narrowed apically but relatively short. The epiphallus is a quite wide, tongue-like structure, barely rounded or curved on the blunt apex. The sharp, basally stout dististyle arises subapically, and has the usual dorso-apical incision and hook. Epandrium also with a deep, broad, wide, ventral incision, and the dorsal margin plane.

Material studied: Many species which the author has collected in the southwestern United States, and other material given him by Mr. Sperry.

Immature stages: Unknown.

Ecology and behavior of adults: Commonly found about isolated clumps of desert flowers, also resting on the foliage or on the ground. The flies are active in the morning in brilliant, hot sunshine, and I have seen the males in pursuit of females around such clumps between Riverside and Desert Center, California.

Distribution: Nearctic: *Lepidanthrax agrestis* (Coquillett), 1887 (as *Anthrax*); *angulus* Osten Sacken, 1886; *campestris* (Coquillett), 1887; *disjunctus* (Wiedemann), 1830 (as *Anthrax*); *inauratus* (Coquillett), 1887 (as *Anthrax*); *lautus* (Coquillett), 1887 (as *Anthrax*); *butzi* (Curran), 1930, subg. *Podolepida*; *morna* Curran, 1930; *proboscideus* (Loew), 1869 (as *Anthrax*); *rufolimbatus* (Bigot), 1892 (as *Epacmus*).

Neotropical: *Lepidanthrax hyalipennis* Cole, 1923; *indecisus* Curran, 1930; *panamensis* Curran, 1930.

Oriental: *Lepidanthrax compactus* Brunnetti, 1920; *transversus* Brunetti, 1920.

Australian: *Lepidanthrax albifrons* Roberts, 1928; *linguatus* Roberts, 1928.

Genus *Mancia* Coquillett

FIGURES 168, 396, 661, 738

Mancia Coquillett, Canadian Ent., vol. 18, p. 159, 1886b. Type of genus: *Mancia nana* Coquillett, 1886, by monotypy.

Odd, quite small, blackish, *Villa*-like flies noteworthy for the character of the axillary cell which is very slender, much reduced in size because of the strongly narrowed condition of the wing toward the base. The anal cell is very widely open, almost or quite as wide at wing margin as the second or third posterior cell. Second vein arising, with backward spur, a little before anterior crossvein. The wing is hyaline, except the extreme base and the subcostal cell and a minute brown cloud at base of anterior crossvein and middle of first basal cell. The face is bluntly, obtusely conical with a stripe of silvery whitish scales running down between the widely separated antenna from the lower part of the front to the anterior edge of the oral recess; proboscis slender, a little longer than the oral recess. The abdomen bears scattered, light reddish brown, narrow, appressed scales and a white band at base of abdomen.

A single species is known from California.

Length: 3.5 to 4.5 mm.

Head, lateral aspect: Nearly globular, the occiput moderately long, but rather strongly rounded inward, the occipital cup large and deep with short, dense fringe which becomes longer dorsally. The pile of the occiput consists of flat-appressed, rather broad, pale, brownish-yellow scales. The front is about twice as wide as the long, swollen ocellar tubercle in the female, and there is a faint groove running forward on each side of the tubercle so that the upper middle part of the front is very slightly depressed. Remainder of front almost flat.

The upper eye corners are strongly rounded and the ocelli are placed a little forward from the posterior mar-

gin of the eye. The pile of the occiput consists of scattered, erect and somewhat curled, bristly, black hairs; and anteriorly, especially in front of each antenna, there is a patch of subappressed, brownish-orange scales with a larger patch of silver scales placed transversely in front of the antenna and continuing on down the middle of the face almost to the oral margin. The face from the lateral aspect is rather prominent, projecting triangularly forward, not quite as far as the tip of the antennal style. In addition to the scales in the middle of the face, scarcely seen laterally, there are scattered, appressed, black and yellow, bristly hairs along the sides of the anterior part of the oral cup. The eye is large, the posterior indentation is rather low, but extensive above and below the midpoint. The facets of the eye diverge at the midpoint of the excavation, but there is no bisecting line. Proboscis rather short, but slender, with slender labellum, the whole proboscis is very little longer than the head and the palpus is quite slender and threadlike. The antennae are placed just above the middle of the head. They are small and short, the first segment quite short and disclike with a few short setae dorsally. The second segment is about twice as long as the first, shorter than wide. The third segment is not quite as wide as the second segment, forming a very small, short, knoblike or bulblike base with a very abruptly formed, long, quite slender style of uniform width with a bristle at the tip.

Head, anterior aspect: Head almost circular, a little wider than the thorax, the face at the antenna comprises a little less than one-third, slightly more than one-fourth of the head width. From the anterior view the ocellar tubercle is high, prominent, abruptly formed, and the vertex sinks a little below the eye margin. The antennae are widely separated and arise very close to the eye margin. The face below the antenna is very little wider than the front. The oral cup is unusually long and slender with thick walls, pinched in laterally at the middle and comparatively deep throughout, and without medial grooves or ridges anteriorly. Gena narrow, tentorial pit or fissure shallow. Head, viewed from above, with the occipital lobes adjacent and the fissure rather deep.

Thorax: Short and broad with large wide, convex scutellum. The mesonotum is opaque, blackish on the anterior half with thin gray pollen. Posterior half of the scutellum shining. In material I have seen there is a furrowlike medial crease on the anterior half; it may be abnormal. Pile of the mesonotum on the anterior half consists of abundant, erect, shining, white, flattened pile of medium length, but with the very sparse anterior collar composed of longer pile. In addition there is a considerable amount of broad, flat-appressed, yellowish and whitish scales, especially laterally and on the humerus and notopleuron, and the scales on the posterior part of the mesonotum, and on the base side and margin of the scutellum are a little more slender, appressed, and brownish yellow. Mesopleuron with a tuft of radiating bristly pile. Metanotum, metapleuron

with a conspicuous tuft of erect, bristly pile. Hypopleuron and pteropleuron bare. Scales of squama narrow.

Legs: There is a peculiar tuft of very large, long, broad, white scales, extending downward on each side of the front coxa. The legs are small and weak, the hind femur a little thickened and flattened, more stout than the other legs, but in no way swollen. The anterior tibia is smooth, except for 1 or 2 minute, bristly hairs and 3 or 4 even smaller similar hairs ventrally. Middle and hind tibia with 4 or 5 slender, sharp, oblique bristles dorsally on each side.

Wings: Wings hyaline with dark veins and the extreme base and the auxiliary cell yellowish. There is a tiny trace of brown yellow below the origin of the third vein and at the anterior crossvein. The wing is characteristic in shape, being strongly narrowed basally. The axillary lobe is small, short and narrow, and the anal cell open by almost the full length of the axillary lobe, being extraordinarily wide. There are 2 posterior cells. There is scarcely any trace of bend on the second vein. It arises rectangularly a little before the anterior crossvein and has a small backward spur. The anterior crossvein enters the discal cell at the middle. There are only 2 submarginal cells. The first posterior cell, and the others as well, are widest at the wing margin. Ambient vein complete. Alula rudimentary or vestigial. There is a small basal comb.

Abdomen: Short oval, the seventh tergite in the female triangular. Abdomen at the base as wide as the thorax. First tergite with a small patch of erect pile laterally and the posterior margin bearing a fringe of broad, brownish-yellow scales. Second tergite with flat-appressed, radiating, broad, brownish-white scales; it has a few brown scales on the posterior margin. Third to sixth tergites with numerous brownish-orange, broad, appressed scales laterally which are apt to be denuded centrally. Terminal, concealed tergites yellowish orange with fringe of long, shining whitish hairs. I have seen only the female. The next to the last sternite has a curious, conspicuous postmarginal band or fringe of long, broad, silvery or yellowish-white scales.

Material available for study: A representative of the type-species.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Nearctic: *Mancia nana* Coquillett, 1866.

Genus *Neodiplocampta* Curran

FIGURES 167, 189, 392, 657, 658, 669, 743

Neodiplocampta Curran, Families and Genera of North American Diptera, pp. 193, 200, 1934. Type of genus: *Diplocampta roederi* Curran, 1931, by original designation.

Agitionia Hull, Ent. News, vol. 77, pp. 225-227, 1966. Type of subgenus: *Agitionia septia* Hull, 1966.

Flies rather less than medium size in this family and with the face short to long conical or even bluntly pro-

tuberant and slightly convex below the antenna. They can usually be readily distinguished by the brown or yellowish-brown anterior border upon the wing with brown mottlings upon crossveins and vein furcations coupled with the strong sigmoid bend of the second vein. At least one species has the wing unusually broad, almost entirely sepia brown, the bend in the second vein unusually strong. From *Dipalta* Osten Sacken, to which it is related, it is separated by the presence of only 2 submarginal cells. From *Chrysanthrax* Osten Sacken, to which it also seems related, it is separated by the distinct double bend in the second vein.

There is one subgenus, *Agitionia* Hull (1966), distinguished by the very broad or wide, large wing, larger size, second vein more strongly contorted, more elongate abdomen, etc. The wing is almost entirely deep sepia in color. Found in southern Brazil.

Neodiplocampta is a small genus ranging from southern South America to Mexico, the West Indies, and the southwestern United States.

Length: 5 to 11 mm.; wing 5 to 11 mm.

Head, lateral aspect: Head hemiglobular, the occiput only moderately long in lateral profile and a little shorter ventrally. The pile consists of long, slender, flat-appressed scales of a yellowish color. The central fringe around the occipital cup is dense and short. The eye is reniform with the posterior indentation shallow, but broad. The eye facets are rather uniform in size, and there is a very short bisecting line extending forward from the bottom of the indentation.

In some species the scales of the occiput are more sparse, and intermixed with them are some fine, black, more or less erect setae. The front is long and slightly raised in front of the antennae, covered with numerous, fine, nearly erect, bristlelike hairs and also with numerous, broad, more or less appressed, spear-shaped, yellowish scales, which vary considerably in number and size in different species. The face is strongly peaked triangularly and conically forward with black bristly hairs similar to those of the front, but more or less appressed, and with, in addition, scales similar to those of the front but of varying density. Sometimes the face is completely covered with a mat of these scales and the bristly hairs may form a fringe overlapping the edge of the oral cavity. In addition there is a bare, pollinose band, rather narrow, free of pile and scales, encircling the upper face and reaching to the base of each antenna, but not extending across the middle of the face.

The proboscis is comparatively slender, the labellum long, slender and pointed, and usually the tip of the labellum barely extends beyond the peak of the oral recess. However, in one species the entire labellum extends forward beyond the peak of the face. The palpus is rather long and filiform, often curled, with a row of stiff, erect setate hairs ventrally and laterally. The antennae are attached a little above the middle of the head. They are comparatively small, the first segment is a little widened apically, twice as long as its apical width, and bears numerous bristly setae or short,

bristly hairs. Second segment wider than long, broadly attached to the third segment, but with rounded lateral margins. Third segment with a bulbiform, conical base stretching out into an attenuated style, the whole segment only slightly longer than the first two combined, and the thickness of the style varies in different species, and represents a prolongation of the dorsal part of the third segment.

Head, anterior aspect: Head as wide as the posterior part of the thorax. The eyes are rather narrowly separated in the males by a distance at the vertex not more than twice the width of the second antennal segment. Of this narrow space, the prominent convex ocellar tubercle, with nearly vertical sides, occupies at least four-fifths. The ocellar tubercle is set near, but not at, the posterior eye corners and it is not quite equilateral in form. From the lateral aspect it is almost hidden by the upward overgrowth of the eyes; posterior eye corners slightly rounded. Face and lower front comparatively wide, the face strongly convergent below. The head is nearly circular from the front view. The antennae are widely separated, but distant from the eye margin by a little less than the length of the comparatively long first antennal segment. The oral recess is long and slender and quite deep, the posterior wall is a little thickened, although its edge is sharp, and the drop down below the eye is a short distance only. The wall of the oral cup is thickened in the middle, and again thinned and narrowed anteriorly. The gena is linear and there is a very shallow, linear, tentorial crease. Viewed from above the occipital lobes have a vertical fissure rather than a horizontal one and the lobes are scarcely touching.

Thorax: The mesonotum is slightly convex, black, more or less shining with brown pollen which may be quite faint or quite dense. The mesonotum is a little wider posteriorly and either sparsely or densely covered with fine-appressed pale hair in some species, and in other species, distinct scaly hair. The anterior collar of pile is stiff, blunt-tipped, but comparatively short and loose, and grading back into the pile of the mesonotum. Notopleuron and sides of mesonotum with very weak, slender bristles, sometimes yellow, sometimes black and those of the notopleuron occasionally more stout. Postalar callosity and the margin of the scutellum with a few slender bristles and bristly hairs. Disc of scutellum colored and clothed like the mesonotum. The whole of the mesopleuron covered with stiff bristly hair. The pteropleuron, the metapleuron, the sides of the metanotum, and the plumula, all with abundant, long, stiff pile. There is a tuft of hair beneath the haltere. The whole of the hypopleuron is bare. Scales of the squamal fringe short.

Legs: The legs are only moderately strong, the front pair reduced, and the front tarsi nearly smooth, having only fine, minute appressed setae dorsally. The anterior femur may have a few fine, short bristles dorsally. Middle femur has 1 to 3 rather stout bristles in the

middle anteriorly, and the hind femur has 3 to 6 bristles of varying size, some of them stout, on the anteroventral margin. Middle and hind tibia with fine, slender, oblique bristles, stouter on the hind legs, placed in 4 rows. There are 6 or 8 bristles anterodorsally on the middle tibia, 6 to 10 on the posterodorsal row, 6 to 10 on the posteroventral row, but only 5 or 6 anteroventrally. Hind tibia with the numbers similar, but the bristles stouter, and in some species with somewhat greater numbers on the dorsal rows, claws small, sharp, almost straight and pulvilli absent.

Wings: Of moderate width, and almost as wide apically as basally. There are 2 submarginal cells and the distinctive feature of the wing lies in the very strong, double bend or sigmoid kink in the second vein. The first posterior cell is a little narrowed. The anal cell is widely open in most species, narrowly open in some. The alula is present but not very wide. The ambient vein is complete. Costal comb present but narrow. Costal hook sharp and thornlike. The second vein arises opposite or shortly in front of the anterior crossvein or shortly beyond. The anterior crossvein enters the discal cell before or at the middle.

In some species the wing is broadly oval or even extremely wide and large and the abdomen distinctly more elongate than the type-species from the Nearctic and the second vein much more strongly contorted. Such species have been relegated to the subgenus *Agitionia* Hull.

Abdomen: Short oval, varying from almost entirely brownish yellow or red with the first tergite and a triangle on the second blackish to other species in which there is greater proportion of black down the middle of the abdomen or species in which the abdomen is wholly black. The pile consists of a dense covering of slender, appressed scales, or scaly pile, intermixed with subappressed, black setae. These setae form a scanty fringe along the lateral margins of the tergites. The stiff pale pile on the first tergite may extend completely across the segment or be absent in the middle, or may extend on to the basal corners of the second tergite, or be absent from this area and replaced by a few, stiff, black hairs. There are 7 tergites visible. The male terminalia are small, asymmetrical, short conical. The females have a fringe of spines on each acanthophorite.

Material available for study: Several species collected by the author and by Dr. W. G. Downs in Mexico and in the southwestern United States.

Immature stages: Unknown.

Ecology and behavior of adults: These flies frequent low-growing flowers in arid regions. They can also be found resting upon the ground.

Distribution: Neotropical: *Neodiplocampta paradoxa* Jaenicke, 1867; *roederi* Curran, 1931; *sepia* Hull, 1966 (as subg. *Agitionia*). I have 6 new species before me that are included in a new manuscript.

Genus *Paravilla* Painter

FIGURES 176, 184, 407, 707, 717, 951, 952

Paravilla Painter, Journ. Kansas Ent. Soc., vol. 6, p. 10, 1933a.Type of genus: *Paravilla edititoides* Painter, 1933, by original designation.

This group was erected by Painter (1933) for all those species of the old *Villa* Lioy complex that have the front tibia spinose and the face conically projecting. In *Paravilla* the face is quite conical, distinctly more conical than in either *Hemipenthes* Loew or *Chrysanthrax* Osten Sacken. The front tibiae are distinctly spinose; the pulvilli are absent. The basal part of the wing is diagonally dark and never with lighter fenestrate spots about the crossveins and furcations. Finally, it should be noted that the fourth posterior cell has only punctiform or nearly punctiform contact with the discal cell and the latter is obtuse at the apex.

As far as is known, *Paravilla* Painter is a New World group of rather numerous species.

Length: 5 to 15 mm., mostly flies about 10 mm. in length.

Head, lateral aspect: The head is hemiglobular, however, with the face sharply and conically produced. The occiput is extensive, both above and below, but strongly retreating inward from the eye margin at a strong, rounded, oblique slant so that the curvature of the eye is continued back over the occiput. The pile is dense and consists of appressed scaliform pile or slender scales or both; central fringe around the occipital recess is short. The eye is large and only slightly concave posteriorly since the posterior indentation is shallow though extensive. There is a short bisecting line at the bottom of the indentation along the posterior eye margin. The front is comparatively flat, often a little sunken midway between the vertex and antenna and slightly raised in front of the antennae. The pile is very coarse and bristly and erect, generally black, and characteristically there are numerous scales that are mostly slender, ranging from erect to appressed or subappressed. Both pile and scales are continued onto the sharply peaked conical face. The bristly setae, however, on the face become rather strongly appressed and also form a scanty fringe extending beyond the margin of the oral cup and generally somewhat concentrated medioapically at the tip of the face. The face is as extensive as in *Dipalta* Osten Sacken or *Stonyx* Osten Sacken or perhaps even more prominent. It may extend almost to the apex of the antennal style, and the total length of the face from eye margin to apex is nearly equal to the total length of the antenna. The antenna is set forward from the eye margin a distance equal to the length of the second segment.

The proboscis is slender with long, slender, pointed labellum, and extends beyond the length of the oral cavity by not more than the length of the labellum; more commonly merely the tip of the labellum protrudes beyond the length of the apex, or is even shorter

than the oral cavity. The palpus is slender, long, cylindrical, often curled with a fringe of stiff hairs laterally and ventrally. The antennae are attached distinctly above the middle of the head, not far from the upper third of the head. They are short; the first segment is equal to twice as long as wide, and it is somewhat swollen and widened apically. The second segment is beadlike, scarcely as long as wide, rather broadly attached to the base of the third segment. The third segment is elongate conical in which the more narrow unsegmented stylelike portion varies in length from one-third to one-half of the total length of the segment. The first segment bears numerous short bristles on all sides, sometimes absent, sometimes present below. In length these bristles are usually a little longer than the second antennal segment. Second segment with short setae dorsally and laterally.

Head, anterior aspect: The head is not quite as wide as the posterior width of the thorax. It is nearly circular. In males the eyes are separated by the length of the first two antennal segments or about twice the width of the antennal tubercle. The antennal tubercle is placed near the slightly posterior eye corners, and laterally the eye rises above the tubercle. At the antennae the face is slightly more than twice as wide as the width of the vertex of the head. The antennae are widely separated and are distant from the eye margin by not more than and usually less than the width of the first segment. The oragenal cup is long, slender, especially anteriorly, and quite deep, becoming shallow only at the apex of the face. On the anterior half the walls are thickened. Anteriorly the gena is completely linear with a very long linear tentorial crease that extends backward nearly to the bottom of the eye, at which point the gena is a little more extensive, extending downward from the eye. Viewed from above, the occipital lobes are tightly apposed, the fissure more vertical than horizontal and with a wider fissurelike pit behind the ocelli.

Thorax: The thorax is slightly wider posteriorly, the postalar callosities wide and shelflike, ground color black, but usually with brown, gray, or yellowish pollen present and not infrequently greenish pollen. The anterior collar varies from loose and sparse with mostly pointed hairs to other species where it is more dense with blunt hairs. Pile of the mesonotum is matted, appressed, scaliform with more bushy pile lying appressed over the wing and anteriorly to the humerus. In addition, in many species there are very fine, erect and suberect, black or yellow bristly hairs. Notopleuron, the postalar callosity, and the margin of the scutellum with weak bristles of increasing length. The scutellum is clothed like the mesonotum, comparatively flat with nearly hemicircular rim. The propleuron, the mesopleuron, and almost the whole of the metapleuron have conspicuous tufts of long, coarse, bristly pile, usually pale, but sometimes black in color. Pteropleuron with considerable pile, a conspicuous patch of shorter pile above the posterior costa. There

is a tuft of hair beneath the haltere; the anterior hypopleuron above the middle coxa is bare, and the squamal scales are rather long and conspicuous.

Legs: Relatively strong including the front pair which are smaller but not greatly reduced. First four femora slightly widened toward the base. Hind femur stout and of uniform thickness. The anterior femur has 3 to 5 bristles near the middle anteroventrally. They may be quite stout. Hind femur with 3 to 5 bristles, sometimes stout and sometimes rather small, along the anteroventral margin. Surface of femora and tibiae with rather broad, conspicuous scales. Characteristically the anterior tibiae bear spicules or short bristles, usually 5 to 7, along the anterodorsal and posterodorsal margins. Middle and hind tibiae with more conspicuous, sharp, oblique bristles in 4 rows together with some small setae. There are usually 6 to 8 bristles in these rows excluding the shorter setae. Claws large, even anteriorly, slightly and gradually curved from the base, pulvilli absent.

Wings: Large, comparatively elongate and generally slender, a little pointed apically, sometimes broader at the base. Approximately the outer half of the wing diagonally is hyaline or subhyaline, with or without an occasional small spot at the more distal furcations of veins. Usually the dark pattern and spots are gently suffuse instead of sharply marked; however, this varies considerably and in species like *castanea* Jaenicke, there is an exceptional pattern of 3, irregular, sharply-defined spots across the wing, one at the base, one at the middle, one apical with supplementary spots. Characteristically, the contact of the discal cell with the fourth posterior cell is nearly punctiform or at least short. The anal cell is open. First posterior cell rarely narrowed strongly, usually only slightly narrowed. The anterior crossvein enters the discal cell at the middle or before the middle of the cell, and the second vein arises at shortly before or shortly after the anterior crossvein. The ambient vein is complete and the alula is relatively narrow.

Abdomen: As wide, or sometimes distinctly wider than the thorax, especially in females. Ground color usually black with terminal tergites sometimes yellowish. The pile varies from dense mats of flat-appressed hair, in some species slightly scaliform hair, and other species in which appressed pile is more sparse, although sometimes forming distinct bands along the posterior margins of the tergites. Most species have considerable amounts of fine, erect pile, a little longer toward the base of the abdomen, yellowish, or sometimes intermixed with black. Males of some species have the last two tergites with appressed silvery scales. In species like *castanea* Jaenicke there may be more bushy pile than appressed pile on the dorsum of the abdomen. Female terminalia with 8 pairs of slender, slightly spatulate spines on the sides of the acanthophorites. Male terminalia asymmetrical, more or less recessed, obtusely conical.

The male terminalia from dorsal aspect, epandrium removed, show a structure wide basally, narrowed apically; the epiphallus is extremely broad, long and tongue-like. The basal part of the aedagus is large and subquadrate; lateral apodemes leaflike, and paired. From the lateral aspect, the dististylus is distinctly subapical, has a dorsoapical incision and hook. The epiphallus is conspicuous, and thick and long. The epandrium triangular with extensive downturned basal lobe.

Material available for study: Nearly 40 species, mostly collected by the author and his wife.

Immature stages: The host preferences for only a few species are known. See discussion under life histories.

Ecology and behavior of adults: These flies are readily attracted to a number of species of flowers, mostly to the composites.

Distribution: Nearctic: *Paravilla apicola* Cole, 1952; *castanea* (Jaenicke), 1867 (as *Anthrax*); *cinerea* Cole, 1923; *consul* (Osten Sacken), 1886 (as *Anthrax*); *coquillettii* Painter, 1965 [= *obscura* (Coquillett)], 1894 (as *Anthrax*); *cunicula* (Osten Sacken), 1886 (as *Anthrax*); *diagonalis* (Loew), 1869 (as *Anthrax*); *edititoides* Painter, 1933; *emulata* Painter, 1962; *epheba* (Osten Sacken), 1886 (as *Anthrax*); *extremis* (Coquillett), 1902 (as *Anthrax*); *flavipilosa* Cole, 1923; *fulvicoma* (Coquillett), 1887 (as *Anthrax*); *fumida* (Coquillett), 1887 (as *Anthrax*); *lacunaris* (Coquillett), 1892, (as *Anthrax*); *mercedis* (Coquillett), 1887 (as *Anthrax*); *nigrinasica* Painter, 1933; *pallata* (Loew), 1869 (as *Anthrax*); *perplexa* (Coquillett), 1887 (as *Anthrax*); *separata* (Walker), 1852 (as *Anthrax*) [= *nemakagonensis* (Graenicher), 1910 (as *Anthrax*)]; *spaldingi* Painter, 1933; *syrtis* (Coquillett), 1887 (as *Anthrax*); *tricellula* Cole, 1952; *vastus* (Coquillett), 1892 (as *Anthrax*); *vigilans* (Coquillett), 1887 (as *Anthrax*); *xanthina* Painter, 1933.

Genus *Poecilanthrax* Osten Sacken

FIGURES 180, 190, 198A, 417, 710, 720, 948, 949, 950

Poecilanthrax Osten Sacken, Biologia Centrali-Americana, Dipt., vol. 1, p. 119, 1886. Type of genus: *Anthrax ateyon* Say, 1825. Designated by Coquillett, p. 593, 1910, the first of 7 species.

Cole (1917), pp. 67-78, key to 22 species (as *Anthrax*).

Maughan (1935), pp. 53-56, key to 13 species from Utah and western states.

Johnson and Johnson (1957), pp. 2-5, key to 27 species and subspecies.

Painter and Hall (1960), pp. 19-25, key to 36 species and subspecies.

A genus of large flies; only an occasional individual is reduced in size. They may be recognized by an ensemble of characters: the most outstanding are the large, elongate, pictured wings, the presence of 2 or rarely 3 submarginal cells, the emission of vein M2 from well in front of the lower outer angle of the discal

cell, and the lower outer angle usually bearing a prominent spur vein. To the characterization may be added the fact that the abdomen is moderately lengthened, the face is sharply to bluntly conical, and the proboscis projects a little way beyond the oral recess or is entirely confined to it. The front tibia is smooth and its tarsi reduced, the pulvilli absent. Vestiture consists of sparse, rather stiff hair, scales absent. While the wing patterns are characteristic and conspicuous, they tend to be distinctly diffuse along the edges of the patterns; a few species have merely the foreborder of the wing darkened with yellow or brown to the end of the marginal cell.

Poecilanthrax Osten Sacken is primarily a Nearctic genus with most species western and not a few species extending down into northern Mexico.

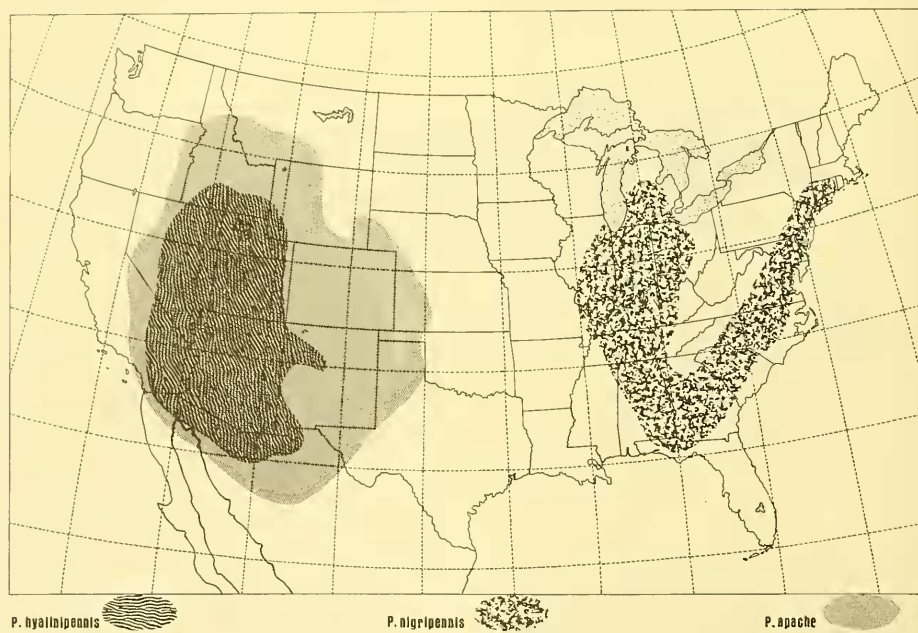
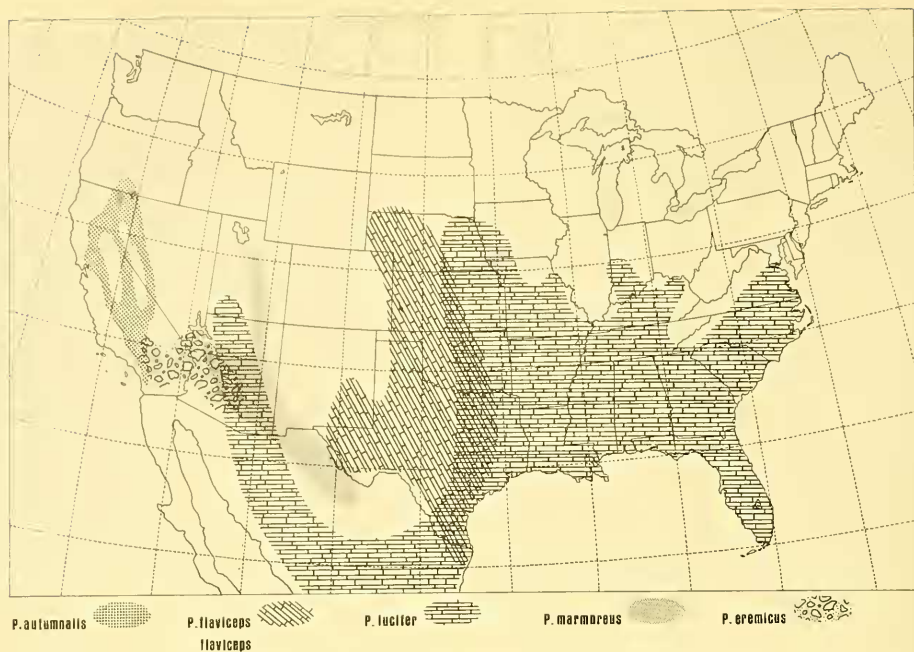
Length: 8 to 14 mm.; wing, 8 to 17 mm.

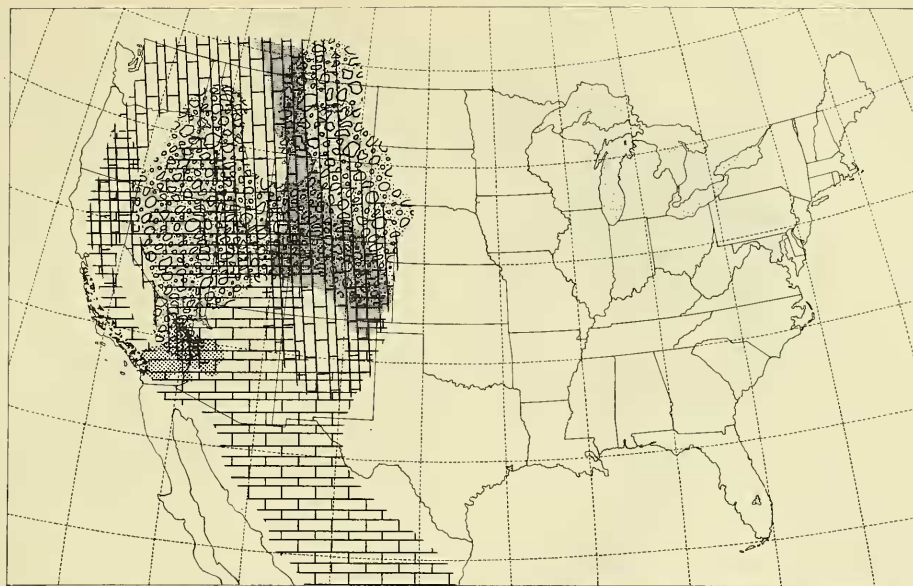
Head, lateral aspect: Head hemiglobular, a little shorter than in some related forms, and the occiput, though well developed, is shorter and slopes inward much more rapidly at a strong slant. Hence the occipital fissure is vertical rather than horizontal. The surface of the occiput is strongly pollinose, usually pale gray, and the pile short, rather fine, suberect and directed forward to the eye margin. The pile is rather loose and scanty. The eye is slenderly reniform with

an exceptionally broad excavation that extends from near the bottom of the eye to close to the top of the eye. At the bottom of the indentation the eye facets curve forward toward the front of the head for a short distance, but there is scarcely any trace of a definite bisecting line. The front is slightly raised and a little more so in front of the antenna. It is dully shining without evident pollen, except across the vertex, and the pile is abundant, sometimes fine, sometimes coarse, erect, and never as long as the first antennal segment. The ground color varies from pale yellow to dark reddish brown and changing to black at the vertex. Face produced forward as a short, triangular cone in most species, but with a varying degree of obtuseness; thus, for example, in *californicus* Cole it is less sharply peaked than in *demogorgon* Walker or as in *flaviceps* Loew. The pile of the face which is pale in ground color consists of scattered bristly hairs, black or pale or both, a little more curled and appressed and less erect than the pile of the front, and less numerous beneath the antenna. There is in fact a narrow, encircling band beneath the antenna that is bare of pile. Some hairs extend over the margin of the oral recess and there is often a cluster of dense setae, black or pale, concentrated medially at the apex of the peak of the face.

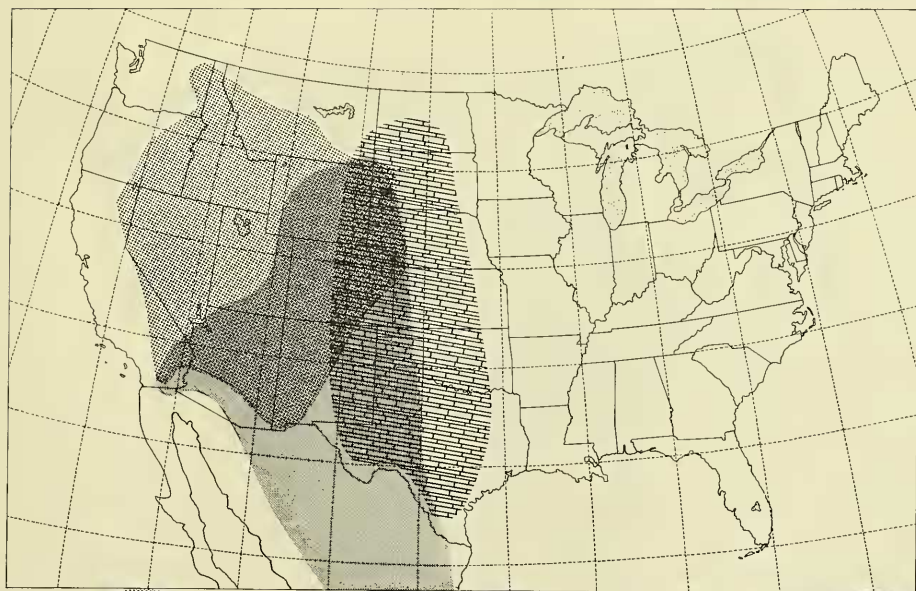
Representative definitive distribution patterns and ranges of species of *Poecilanthrax* Osten Sacken. Adapted and redrawn from Painter and Hall.







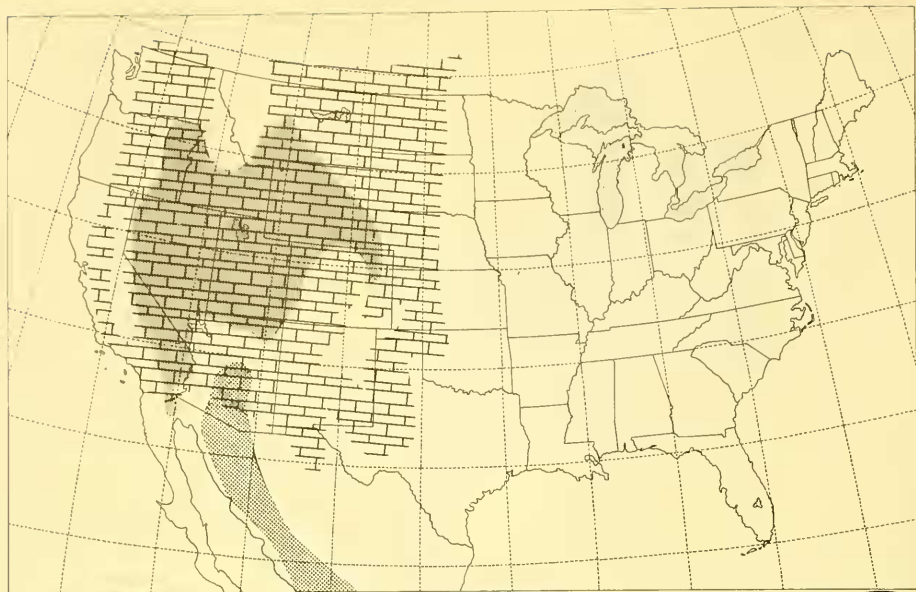
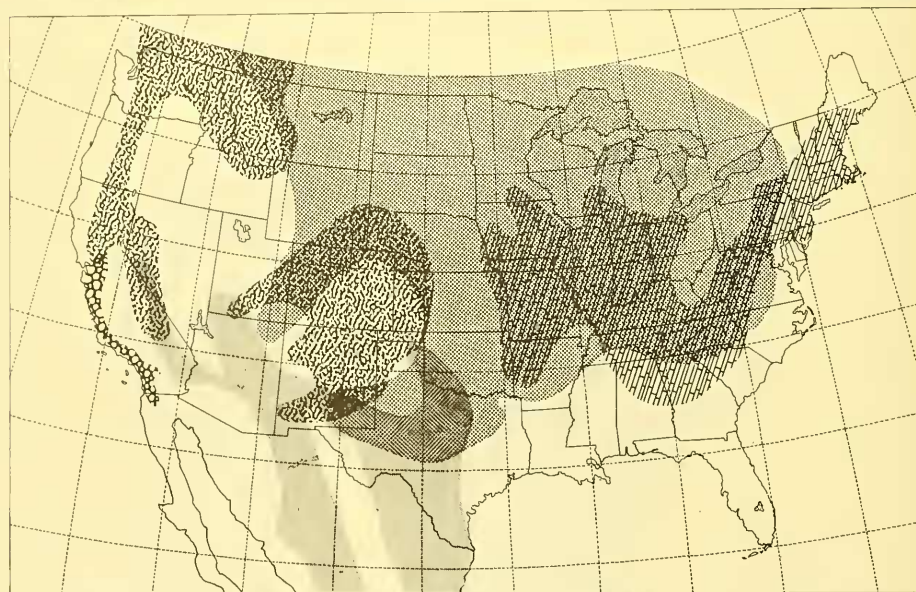
P. poecilogaster poecilogaster *P. signatipennis* *P. tanbarkensis* *P. poecilogaster interruptus* *P. sackenii monticola* *P. sackenii sackenii*



P. californicus

P. fasciatus

P. arethusa

*P. varius**P. vexativus**P. willistonii**P. littoralis**P. effreus**P. alcyon**P. alpha**P. coxii*

The proboscis and labellum are slender. The tip of the latter extends just beyond the apex of the face. Palpus slender, almost filiform, not quite half as long as the proboscis and bearing only extremely fine hairs scattered along the lower and lateral margin. The antennae are attached slightly above the middle of the head and are relatively small and slender. The first antennal segment is very distinctly widened medially at the apex. It is about $2\frac{1}{2}$ times as long as its basal width, and $3\frac{1}{2}$ to 4 times as long as the small beadlike second segment. The first segment bears considerable coarse, bristly hair, black or yellow, over the whole lateral, dorsal and medial surfaces; but these tufts are accentuated on each side and the segments are bare ventrally. The second segment, however, has a complete ring of appressed setae. Third segment not wider than the second, elongate conical with the base bulblike and extending rather gradually into the attenuate style, so that beyond the swollen base the middle third is considerably thicker than the apical third. Apex with a minute spine. The third segment, style included, is very slightly longer than the first two segments; in a few species it is of equal length, and the style is an attenuate continuation of the dorsal part of the segment.

Head, anterior aspect: The head is distinctly wider than the anterior thorax, but about the same width as the posterior part. It is nearly circular, slightly flattened on all four sides with the eye and at the vertex distinctly raised above the vertex, almost obscuring the ocelli when viewed from the side, and the small ocellar triangle has vertical sides, is extended backward as a low ridge. The ocelli themselves occupy a short isosceles triangle and are characteristically placed far forward from the posterior eye corners. Eyes in the male separated by a little more than 3 times the width of the ocellar tubercle and in the female by 4 or more times the width. The antennae are set rather far apart. They appear a little closer together because the first segment is convergent and they are separated from the eye margin by nearly the length of the first antennal segment. The oral recess is narrow and deep, especially posteriorly, with vertical walls, and on the anterior half the lower edge is rounded and inflated, the margin sharp beneath the eye. The genae are narrow, separated medially by a deep though narrow crease, and they become a little more extensive at the bottom of the eye. From above, the occipital lobes vary in development and also in apposition. The lobes and the tight fissure are almost horizontal or are only a little slanted, whereas in a few species there is a distinct gap between the lobes that do not touch.

Thorax: Shining black with reddish or sometimes bluish-gray pollen. The pile is rather short, flat-appressed, and scaliform, merging anteriorly into a broad collar of stiff, rather pointed pile. The pile is longer in some species, extending fully over upon the humerus, sometimes extending back to the notopleuron,

and merged with the dense tufts of pile on the upper mesopleuron. The pile above the wing is coarse, sometimes rather long and matted, in other species consisting only of a few, short, curled, bristly hairs as in *demogorgon* Walker. The notopleuron has some short, stiff bristles. There are 4 to 6 bristles on the postalar callosity, and the margin of the scutellum has short, slender, weak bristles, longer in a few species. Disc of scutellum coated with appressed hair similar to the mesonotum, but apt to be denuded posteriorly. Mesopleuron, pteropleuron, and metapleuron, and the upper sternopleuron with much dense pile, finer and shorter on the sternopleuron, longer, coarser, almost bristly on the upper mesopleuron. There is a patch of erect hairs on the hypopleuron above the posterior coxa, and a tuft of hair beneath the haltere. Anterior hypopleuron bare. Plumula pilose, scales of the squama quite short, poorly developed, a few extending onto the alula.

Legs: Moderately developed, the anterior pair reduced in size, and its tibia smooth. Middle femur with a row of slender bristles along the middle anteriorly, and usually with a few bristles also posteriorly, 3 to 6 in each row and variable in size. They are rather prominent in *californicus* Cole. Hind femur with 6 to 9 bristles anteroventrally and with 4 or 5 dorsally near the apex in some species. Hind tibia with conspicuous, long, sharp, oblique bristles in 4 rows. There are 7 to 9 anteroventrally, about 13 in the anterodorsal row excluding the shorter setae, and about the same number dorsomedially, but fewer ventromedially. Claws slender, sharp, long, with scarcely a trace of basal tooth and no pulvilli. Anterior claws exceptionally minute.

Wings: The wings are characteristic, large and quite long, extending far beyond the abdomen, not broadened at the base, sometimes slightly pointed at the immediate apex. They are notable for the fact that they are never hyaline but colored by several types of patterns. In some species the apical half of the wing is irregularly pale, tinged by dense villi. In most species the wings are mottled. They may be dark sepia brown as in *demogorgon* Walker and often the cells, especially apically, and the posterior cells become grayish hyaline in the centers, leaving most of the veins diffusely margined with reddish yellowish or blackish brown. In *lucifer* Fabricius the entire wing is nearly uniformly brown. The patterns, while confusing, are distinctive for each species. The second vein arises at or a little before or even beyond the anterior crossvein and the anterior crossvein enters the discal cell usually at, sometimes slightly before the middle of, the discal cell. The contact of the discal cell with the fourth posterior cell is usually about as great as the length of the anterior crossvein, not more, sometimes less, and in one species punctiform. Generally there are 2 submarginal cells, occasionally 3, formed by an erratic crossvein, connecting the posterior branches of the third vein. Generally there are 4 posterior cells, but sometimes 5, formed by an erratic crossvein extending all the way

through the third posterior cell. The first posterior cell is narrowed at the wing margin and may be almost closed. Anal vein widely open.

The alula varies from 3 to 4 times as long as wide to quite narrow in a few species, 8 or more times as long as wide. The ambient vein is complete with short fringe of hair. The costal comb is only moderately expanded, bearing short, fine-appressed setae, and the costal hook small, slender, and sharp.

Abdomen: The abdomen with 7 tergites visible from above. It is narrowly oval, distinctly longer and wider than the thorax, the color varying from black with only small, obscure reddish spots or triangles at the sides of the second and third tergites; even these may be lacking. In other species where a slender triangle of red extends inward from the lateral margin a varying degree toward the middle, leaving the segment blackish in front and behind, except on the margin. In one species the abdomen is entirely fox red, except for a blackish spot of decreasing size on the first 4 tergites. Sides of the female genitalia with a circlet of small slender spines. Male terminalia large with rather long coarse hairs dorsally and apically. The dististyle has a broad base tapering to an apical hook curved sharply inward. I cannot do better than quote Painter and Hall's excellent description of the aedeagus:

The aedeagus is slightly curved from base to apex reaching to beaked apical segments; base broad, gonopore in the middle of aedeagus, elevated projecting inward and upward, the aedeagal struts dorsal of middle part and projecting laterad and above lateral struts; middle part rectangular and not prominent, the lateral struts flange-like, short and broad, the basal strut fan-shaped in profile, prominent, outer edge minutely serrated.

Material available for study: Besides the collection in the National Museum of Natural History, I have extensive material acquired by collecting in six Western States and also in Mississippi.

Immature stages: Hosts are known for 7 species and consist of some 15 species of cutworms, sod worms and armyworms, all from the family *Noctuidae* (*Phalaenidae*). One species has been recorded as a hyperparasite of white grubs. See discussion under life histories.

Ecology and behavior of adults: These flies are abundant on flowers where they feed upon nectar and pollen. Painter and Hall point out that the association is with the group of flowers that happen to be blooming at the time the flies emerge. They note a partiality in the West to various species of rabbit bush, *Chrysothamnus*, and to a lesser extent on *Gutierrezia*, *Grindelia*, and *Senecio*. They note an association in the Eastern Rocky Mountains on resinweed, *Silphium*, and *Asters*, and on the plains species associated with gayfeather, *Liatris*, puncture vine, *Tribulus*, smartweed, *Persicaria*, and goldenrod, *Solidago*. He notes a frequent association with sagebrush, *Artemisia*. In Mississippi species are especially attracted to *Helenium tenuifolium*, and to a lesser extent on ironweed, goldenrod, *Rudbeckia*, *Coreopsis*, fleabane, and sumac.

Distribution: Nearctic: *Pocilanthrax aleyon* (Say), 1824 (as *Anthrax*) [= *halycon* Wiedemann, 1828]; *alpha* (Osten Sacken), 1877 (as *Anthrax*); *apache* Painter and Hall, 1960; *arethusa* (Osten Sacken), 1886 (as *Anthrax*); *autumnalis* (Cole), 1917 (as *Anthrax*); *californicus* (Cole), 1917 (as *Anthrax*); *colei* Johnson and Johnson, 1957; *demogorgon* (Walker), 1849 (as *Anthrax*), [= *ceyx* (Loew), 1869 (as *Anthrax*); *effrenus* (Coquillett), 1887 (as *Anthrax*); *eremicus* Painter and Hall, 1960; *fasciatus* Johnson and Johnson, 1957; *flaviceps* (Loew), 1869 (as *Anthrax*) [= *butleri* Johnson and Johnson, 1957], *flaviceps fuliginosus* (Loew), 1869 (as *Anthrax*); *hyalinipennis* Painter and Hall, 1960; *ingens* Johnson and Johnson, 1957; *johnsonorum* Painter and Hall, 1960; *litoralis* Painter and Hall, 1960; *lucifer* (Fabricius), 1775 (as *Bibio*) [= *fumiflamma* (Walker), 1852 (as *Anthrax*); *marmoreus* Johnson and Johnson, 1957; *moiffiti* Painter and Hall, 1960; *montanus* Painter and Hall, 1960; *nigripennis* (Cole), 1917 (as *Anthrax*); *painteri* Maughan, 1935; *pilosus* (Cole), 1917 (as *Anthrax*); *pocilogaster* (Osten Sacken), 1886 (as *Anthrax*); *pocilogaster interruptus* Painter and Hall, 1960; *robustus* Johnson and Johnson, 1957; *sackenii* (Coquillett), 1887 (as *Anthrax*), *sackenii monticola* Johnson and Johnson, 1957; *signatipennis* (Cole), 1917 (as *Anthrax*) [= *marginatus* Johnson and Johnson, 1959, = *yellowstonei* (Cole), 1917 (as *Anthrax*); *tanbarkensis* Painter and Hall, 1960; *tegminipennis* (Say), 1824 (as *Anthrax*) [= *fuscipennis* (Macquart), 1834 (as *Anthrax*); *varius* Painter and Hall, 1960; *vezatius* Painter and Hall, 1960; *willistonii* (Coquillett), 1887 (as *Anthrax*); *zionensis* Johnson and Johnson, 1957.

Genus *Prothaplocnemis* Bezzi

FIGURE 214

Prothaplocnemis Bezzi, Bull. Soc. Roy. Ent. d'Egypte, vol. 8, p. 220, 1925c. Type of genus: *Argyramoeba anthracina* Becker, 1902, by original designation.

Bezzi based this genus upon the species *Argyramoeba anthracina* Becker, and maintained that this species contained transitional forms to *Aphoebantus* Loew and *Petrossia* Becker. Bezzi placed it, however, as a subgenus to *Anthrax* Scopoli (as *Argyramoeba* Schiner), to which he believed it shows even closer connections, for this species has a plumula. The scutellum is almost triangular with a weakly developed apex, and the abdomen in the female is scarcely longer than mesonotum and scutellum together. The epipygium stands free and is relatively large, but in its parts, it approaches more the characteristic structure for the species of the genus *Anthrax* (*Argyramoeba*). The appendages of the dorsal lamella are still simply hooklike, but the basal lamellae are stretched out and not broad or provided with side lobes. As in the case of *Aphoebantus* Loew, the hairing and scaling of the body is sparse, so that the shining black basic color is very conspicuous. In my figure of the wing the delineation

tion of the brownish black color over most of the wing and the basal hyaline wing areas were omitted.

Material available for study: I have not seen this fly.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic: *Prothaplocnemis anthracina* (Becker), 1902 (as *Argyramoeba*); *persica* Paramonov.

Genus *Pseudopenthes* Roberts

FIGURES 196, 393, 668, 676

Pseudopenthes Roberts, Proc. Linnean Soc. New South Wales, vol. 53, p. 132, 1928a. Type of genus: *Pseudopenthes fencstrata* Roberts, 1928, by original designation.

A small to medium-sized, shining black fly, the wings almost wholly dark brownish black but with the greater part of the second basal cell and the basal half of the third basal cell quite hyaline. The front and face has iridescent whitish scales and on the abdomen the anterior corners of the second and third tergites and the posterior corners of the remaining tergites have patches of white scales giving way abruptly to violaceous black scales.

This genus has the third antennal segment much as in *Villa* Lioy, *sensu lato*, but has 3 submarginal cells as in *Stonyx* Osten Sacken; I do not consider it closely if at all related to these. *Pseudopenthes* Roberts also has a long, sharp, pale colored, basally stout tooth at the base of the claw as in *Exoprosopa* Macquart and *Litorrhynchus* Macquart. The face is bluntly conical with apex rounded, and the ocellar tubercle is set a considerable distance forward from the rear of the vertex. Proboscis quite short, rather stout, labellum fleshy, both confined to the oral recess. The relationship is perhaps closest to *Exoprosopa* Macquart.

A single species is known from South Australia, New South Wales, and Queensland. I collected a single male about midday north of Queensland on a hot, sun-baked open space about a large anthill in bottle-tree country.

Length: 10.5 to 12 mm.; wing 11 to 11.5 mm.

Head, lateral aspect: Head subglobose, the occiput comparatively short, the occipital cup deep, but relatively small. In the male the front is slightly swollen and raised above the eye margin, rather flattened in the middle, and the pile consists of rather loose comparatively short, erect, stiff, black hairs, more numerous on the lower half. Pile of the occiput, minute, subappressed and setate, but with scattered, completely appressed, small silvery scales in addition to the setae and more numerous at the indentation. The face is triangularly produced forward, slightly rounded at the apex of the oral cup. It bears scanty, scattered, stiff, sharp, subappressed black setae, and also appressed silver scales. The lower front, likewise, has appressed silver scales. Proboscis short, stout, with stout, fleshy labellum, which extends slightly beyond the oral recess. The long, slender palpus is cylindrical, of equal width

throughout, and has some very short erect pile. The antennae are attached a little above the middle of the head. They are small and short. The first segment is twice as long as wide with distinctly abundant, fine, oblique or subappressed setae, the hairs about as long as the second antennal segment. Second antennal segment beadlike, slightly less than half as long as the first segment. Third segment triangular at the base, rather strongly attenuated, especially on the lower part, into a thick style with minute bristle, no microsegment, the length of the style about equal to the length of the first segment. The eye is slightly reniform. The posterior indentation is shallow but quite extensive above and below and with a short bisecting line. Facets of the male eye quite small above and below, but wider in the middle anteriorly, and again along the posterior margin on the lower half.

Head, anterior aspect: Nearly circular, wider than the thorax, the antennae widely separated by nearly twice the distance of the first segment to the eye margin. Oral recess wedge-shaped, narrowed anteriorly, long and slender, exceptionally deep, the walls thick, particularly on the anterior half where they are even slightly widened or inflated, though with an anterior or ventral ridge. The tentorial crease, or fissure is long and distinct, the gena quite narrow. The head from above has the occipital lobes slightly separated, rounded and divergent with a 5-grooved, radiating sunken depression behind the vertex.

Thorax: Thorax short and broad, narrowed anteriorly with large, long scutellum, the mesonotum only gently convex, shining black, with dense, small, wide, short, flat-appressed, purplish, black scales, and with a long, lateral, matted border of subappressed, coarse, white pile including the humerus and running to the base of the scutellum. Anterior collar of pile, rather dense, coarse, white, of several rows, and set rather far forward. There are no bristles on the mesonotum. Mesopleuron with a large, dense tuft of erect, coarse, black, bristly pile directed outward. Pteropleuron and hypopleuron bare. Metapleuron with a tuft of bristly hair. Squama with narrow white scales.

Legs: All the femora are a little stout, especially middle and hind pairs, but not swollen. The first four have only a few fine hairs ventrally, hind femur with 3 short, oblique, small, spinous bristles on the outer half. Anterior tibia smooth. The tarsi small. Middle tibia with 4 fine, oblique bristles ventrally, and with 6 or 7 small setae above. Hind tibia with 6 or 7 small, oblique bristles ventrally, but with about 20 short, small anterodorsal, spinous setae, and 12 or 14 posterodorsally. Claws nearly straight, slightly curved at the apex.

Wings: Large and unusually broad, strongly tinged with sepia brown, the middles of the cells faintly paler, but with most of the second, half of the third, and half of the axillary lobe completely hyaline. There are 3 submarginal cells and the posterior branch of the second vein makes a strong rectangular, but rounded, bend

outward. The apex of the marginal cell is greatly swollen backward so that the first submarginal cell is foot-shaped. The second vein arises abruptly with rounded bend opposite the anterior crossvein, and the anterior crossvein enters the discal cell distinctly before the middle. Anal cell widely open, the axillary lobe large and the alula large. Costal comb wide. Ambient vein complete.

Abdomen: Elongate, $1\frac{1}{2}$ times as long as the thorax, the sides nearly parallel and only slightly narrowed posteriorly. The abdomen is a little flattened in the middle on the first four tergites, but more strongly convex on the side, and 7 tergites are visible in the male. The abdomen is shining black, thickly plastered with minute, purplish, black scales, apt to be denuded in the middle of the segments. The base of the first tergite laterally has a band of erect, stiff, white pile, which is confined to the outer third. The base of the second segment has on each side, laterally a narrow band of white, appressed scales. Remaining tergites have a triangular spot of similar scales, which on the third tergite is basal and is the largest spot, and on the fourth tergite it is in the middle of the lateral margin, and on the remaining tergites it lies in the posterior corner. In the male the terminalia are rather small, asymmetrical, more or less recessed and turned toward the right side. I have not seen the female.

Material available for study: A representative of the type-species.

Immature stages: Unknown.

Ecology and behavior of adults: I captured a single male resting on the side of an anthill in the hot sunshine about a hundred miles north of Brisbane, Queensland.

Distribution: Australian: *Pseudopenthes fenestrata* Roberts, 1928.

Genus *Stonyx* Osten Sacken

FIGURES 200, 429, 708, 718, 960, 961

Stonyx Osten Sacken, Biologia Centrali-Americana, Dipt., vol. 1, pp. 80, 94, 1886. Type of genus: *Stonyx cilia* Osten Sacken, 1886. Designated by Coquillett, p. 609, 1910, the second of 2 species.

Flies of medium size, with 3 submarginal cells. This genus is readily distinguished from *Exoprosopa* Macquart by the absence of a divided antennal style. The third antennal segment is small, onion-shaped, and the stylar portion remarkably long and slender and needle-like with minute apical bristle; in the character of the third antennal segment they remind one of *Lepidanthrax* Osten Sacken; both of these genera have the slender proboscis extending well beyond the oral recess. The anterior tibia has a distinct row of spinules or bristles and the pulvilli are absent.

All the known species have the wings sharply variegated with brown and the discal cell is more or less constricted in the middle. The anal cell is open, and

may be widely open. The pile of abdomen and mesonotum is in large part fine, short, and strongly appressed. Face bluntly projecting.

Three species are known; they range from Panama to Mexico and into Arizona. I have collected 2 species in Mexico.

Length: 7 to 12 mm.

Head, lateral aspect: The head is hemispherical, the occiput rather strongly developed, especially in the middle with the posterior surface plane and flattened, rather than rounded, as far back as the margin of the central recess. The stiff, bristly pile is quite dense, but also quite short, and closely appressed to the surface. The inner marginal fringe is dense, but short. The front is very slightly raised at the eye margin, flattened across the middle, bearing comparatively dense, stiff, erect pile, which is blackish in the type-species and almost as long as the first two antennal segments. In the male the anterior and ventral eye facets are larger than those at the vertex. The eye has a very long, comparatively shallow indentation and is bisected by a line at the middle of the eye. At the deepest point of the indentation there is a small bare triangle. The face is extended forward in a low obtuse triangle, a distance somewhat greater than the length of the first three antennal segments, style excepted. In the type-species the pile of the face is entirely similar in length, color, and relative stiffness to the pile of the front. The pile is a little shorter and somewhat appressed in other species. It is rather thick, extending on down the sides of the face, and reappearing more sparsely on the gena.

Proboscis and labellum slender, the latter pointed, all the surface microsetate under high power. It is at least $1\frac{1}{2}$ times as long as the head and generally thrust straight forward. Palpus long, slender, filiform with conspicuous, loose, erect, scattered stiff hairs. The antennae are attached a little above the middle of the head and are comparatively small. The first segment is a little longer than wide, the second wider than long, and not quite as long as the first segment. The third segment is small, scarcely as wide as the second segment, its base plane, but not tightly attached to the preceding segment. The third segment is distinctly shorter than long, shaped much as a flat onion or bulb in the type-species but forming a short triangular cone in other species. Attached to it near the middle is a very long, slender, abruptly formed, needlelike style, with a short spine at the apex. This long style is $1\frac{1}{2}$ times the length of all the three segments, and is very much like that of *Lepidanthrax* Osten Sacken.

Head, anterior aspect: The head is wider than the anterior part of the mesonotum, but a little more narrow than the posterior part. From the anterior aspect the vertex and sides of the eyes are slightly flattened. In males the eyes are separated by a little more than the length of the first three antennal segments, style excepted, or by more than 3 times the width of the small ocellar tubercle. This tubercle is distinctly raised, isosceles in shape, set forward a little from the poste-

rior eye corners, and the whole surface of the front and vertex is pollinose. All species bear some flattened, slender scales on the front and mixed in with the pile of the face. The type-species has few such scales, but they are dense in other species. The antennae are unusually widely separated, distant from the eye margin by not more than the length of the first segment. The oral recess is large, long, and quite deep, with vertical sides for at least the posterior three-fourths of its length. The lateral margin is thin, set close to the eye, with the gena extending downward, not quite the thickness of the proboscis. There is a pale, bare, circular, pollinose line curving down the sides of the upper part of the face and in some species it can be seen curving medially above and between the antennae, and apparently forming the demarcation of face and antennae. The tentorial pit forms a short, deep fissure, lineally separated from the eye margin at the midpoint of the oral recess. Viewed from above the occipital lobes are deeply sulcate posterovertically and not horizontally as in those species where the dorsal occiput is more extensive.

Thorax: Short, distinctly narrowed anteriorly, becoming broadest across the postalar callosities. The mesonotum is comparatively flat in the middle, but a little raised and convex near the wing and only slightly convex viewed laterally. The scutellum is quite wide, but comparatively short, very slightly triangular, each half a little rounded on the margin, both margin and base rather strongly convex. The mesonotum is opaque, blackish, with a conspicuous anterior fringe, narrow, high, dense and very coarse, the bristly hairs with rather blunt apices. Mesonotum of males sometimes distinct from the female as in the type-species. The pile of the mesonotum in the male may consist entirely of rather short, stiff, pale, erect hairs, longer in front of the scutellum, the anterior collar in the male of one color and a different color in the female. This is also true of the pleural pile. Disc of mesonotum in the female rather densely coated with completely appressed, short, coarse, pale bristly hair, the scutellum likewise. Margin of scutellum with slender bristles and notopleuron with a clump of 5 or 6 short, stout bristles. Pile of mesopleuron quite dense, long and bristly and erect. The anterior pteropleuron bears bristly hair, and there is a dense, vertical fringe of hair on the metapleuron; hypopleuron bare, and no pile behind the posterior spiracle. However, there is a small, curious tuft of hair immediately below the haltere which is appressed downward. Metanotum very short. Squamal fringe quite short, dense, and scalelike.

Legs: The middle and posterior femora are moderately stout, anterior femur rather slender, but both anterior and middle femora a little widened toward the base. The anterior femur sometimes has a few slender, bristly hairs below, quite close to the base. Anterior trochanter inserted in a socketlike joint on the coxa. Middle femur with 2 or 3 distinct, sometimes stout bristles in the middle on the anterior surface. Hind

femur always with 3 or 4 distinct bristles on the anteroventral margin of the distal half. They may be rather stout. All femora with scales. Anterior tibia with 8 to 10 slender, oblique bristles anterodorsally, posterodorsally, and ventrally. Middle tibia with about the same number of somewhat longer dorsal bristles, but with sometimes fewer ventral bristles. Posterior tibia with about the same number of bristles as the middle tibia, a little longer, also oblique, sometimes more stout. Claws sharp, gently curved from the base with short pulvilli.

Wings: Wings large and broad basally, blunt apically with 3 submarginal cells and a strong rectangular posterior bend subapically in both the second vein and the anterior branch of the third vein. First posterior cell slightly narrowed apically, the anterior crossvein rectangular, entering the distal cell distinctly before the middle. Contact of discal and first posterior cells never greater than the length of the anterior crossvein. Anal cell widely open. Costa very strongly widened at the base. Setae of costal comb long, bristly and appressed outward. Costal hook long, sharp, and thornlike. Alula comparatively wide, the ambient vein complete, with a long fringe of villi. Whole wing villose, and in all the species known to me, the basal half of the wing, including all or most of the axillary lobe is obliquely dark sepia in color with a varying amount of additional sharp markings of sepia brown on the outer half of the wing, the pattern differing in different species. The second vein arises either before or after the anterior crossvein.

Abdomen: Abdomen short and broad; gently convex. Surface either shining black or opaque brown, the spikelike erect fringe on the first segment may extend completely across this segment, or be much reduced beneath the scutellum, leaving dense, long tufts only laterally. Surface of abdomen with comparatively dense, slightly flattened pile, but in some species becoming distinctly scalelike on the sixth and seventh tergites. Male terminalia large, asymmetrical, extended downward as a prominent cone. Lateral margins of the tergites with moderately prominent tufts of long, coarse, bushy pile, which sometimes shows alternately contrasting colors.

The male terminalia from dorsal aspect, epandrium removed, show a structure with the epiphallus unusually long, narrowing a little near the middle and with the middle part of the aedeagus large, wide and short oval, and much rounded apically. From the lateral aspect it is much like *Rhynchanthrax* Painter except that the ejaculatory process is well separated from the epiphallus. The epandrium is quite similar. The dististyle is subapical with dorsoapical incision and hook.

Material available for study: I have representatives of the type-species given me by Dr. C. H. Curran, also additional species collected by my late wife and me in our last expedition to Mexico.

Immature stages: Unknown.

Ecology and behavior of adults: Very similar to other species of the *Villa* Lioy and *Exoprosopa* Macquart genera. Found on composites or resting upon the ground.

Distribution: Nearctic: *Stonyx elelia* Osten Sacken, 1886 [= *keenii* (Coquillett), 1887 (as *Anthrax*)].

Neotropical: *Stonyx clotho* (Wiedemann), 1830 (as *Anthrax*); *lacerus* (Wiedemann), 1830 (as *Anthrax*); *melia* Williston, 1901.

Genus *Synthesia* Bezzi

FIGURES 229, 715, 726

Synthesia Bezzi, Ann. South African Mus., vol. 18, p. 130, 1921a.

Type of genus: *Synthesia fucoides* Bezzi, 1921, by original designation.

A comparatively small, blackish, *Villa*-like fly of aberrant character, which is distinguished by the yellowish-brown legs, face, lower front, and apex of abdomen, and coarse appressed pile of the same color, and by several characters that set it apart from most other *Exoprosopinae*. The pulvilli are slender but long and well developed, the anterior tibia has spinules only ventrally. While the posterior eye margin is quite shallowly indented, and there is no bisecting line, many American species of *Villa* Lioy approach this condition and differ little. What is more distinctive, perhaps, is the relatively long and prominent face which bulges outward at the eye margin and is prominent and rounded, not conical; the proboscis is shorter than the oral cavity, stout with stout, fleshy labellum; the antennae do not differ greatly from certain species of *Villa* Lioy before me, but they are set quite far apart.

The second vein arises at a right angle well in front of the anterior crossvein, but removed from the crossvein by less than the length of the crossvein; this position while unusual is matched by other species and genera in the subfamily and is not unique. The basal half of the wings are deeply tinged with yellow.

One species is known from South Africa.

Length: 5 to 10 mm.; if wing approximately 5 to 9.5 mm.

Head, lateral aspect: The head is approximately hemispherical. The occiput is short with the central cup or recess large and deep. Pile of the occiput moderately dense, flat-appressed, and consisting of narrow scales densely clustered along the eye margin; the central fringe is short but rather dense on the upper half of the eye and almost wanting below. The front is flattened, slightly raised above the eye margin on the lower part, and densely covered with appressed and subappressed, long, slender, pale, scaliform hairs. There is also some nearly erect, bristly pile mixed in. The face is bluntly protuberant, rounded in front, extending forward at least the length of the third antennal segment. Its pile is moderately abundant, shining, golden reddish, and flattened. Some of it appears to be merely stiff bristles. All of it is short and subappressed.

The eye is longer just above the middle. The posterior margin bears a very shallow, long (or wide), indentation without any bisecting line.

Proboscis short, thin, and laterally compressed but with a stout, somewhat triangular, short, wide labellum. The whole structure is confined to the oral recess. Palpus quite long and slender. A little flattened and clavate apically with a few, short, bristly hairs toward the apex and some long, white, fine, erect hairs on the basal half. Antenna attached a little above the middle of the head, rather small and short. The first segment is considerably widened apically, particularly toward the medial aspect where it forms almost a rounded lobe. Apically it is as wide as long. The first segment bears a tuft of short, stiff, bristly hairs at the apex both medially and laterally in between. Second segment quite short, wider than long, but with a rounded margin. Third segment bulblike at the base, no wider than the second segment and with an asymmetrical, dorsally placed, bristle-tipped, micropubescent style. The style is 3 times as long as the base of the segment and is a little thickened on the basal third.

Head, anterior aspect: The head is slightly flattened dorsally and likewise on each side; it is fully as wide as the thorax. The eyes are separated in the male by a little less than 3 times the ocellar tubercle and the vertex is slightly narrowed in front of the ocellar tubercle. The ocellar tubercle is rather high, the ocelli placed marginally and in an isosceles triangle. The antennae quite widely separated, distant from the eye margin by no more than the length of the first segment. The width of the face at the level of the antenna is a little greater than one-third the total head width. From the anterior aspect the oral recess occupies the lower fourth of the head and is relatively ventral in position. It is elongate with the anterior half comparatively shallow with sloping sides. Posteriorly the walls are vertical. The genae are narrow, separated from the wall of the oral cup by a fissurelike crease with a deep tentorial pit anteriorly. Viewed from above the occipital lobes are adjacent but rounded inward (forward) from behind and the fissure is deep.

Thorax: Comparatively short. The mesonotum is distinctly convex anteriorly, feebly shining blackish in color with dense, flat-appressed, matted, slightly flattened, pale pile and with a few suberect hairs in front of the scutellum, elsewhere on the dorsum and with rather dense tufts of somewhat longer, shining reddish-yellow pile on the whole of the humerus extending back to the base of the wing. Bristles are absent, but the tuft of pile on the notopleuron is dense, more distinctly flattened. The scutellum is quite large, largely pale reddish brown in color with the base blackish and with pile similar to the mesonotum. The marginal hair slightly bristly on the sides, very short in the middle. The anterior collar is distinct but narrow, coarse, moderately long and dense. Propleuron, upper half of sternopleuron, whole of mesopleuron with much coarse, rather long, shining, bristly pile thrust upward on the

mesopleuron and outward collarlike on the propleuron. Pteropleuron and hypopleuron with thin pollen only. Metapleuron, however, with a scanty tuft of long, coarse, hair over the whole posterior half. Squamal scales scanty and narrow. There is a fanlike fringe of conspicuous pile beneath the postalar callosity and the lateral metanotum is pilose.

Legs: The legs are weak, especially the front pair. Anterior femur with 1 or 2 tiny setae. Middle femur with 2 distinct, slender bristles anteroventrally on the outer half and hind femur with a row of 5 to 7 equally slender, oblique bristles anteroventrally. Anterior tibiae smooth, their tarsi small and short, middle tibia with 4 or 5 small anteroventral bristles, slender and sharp, and the same number in each dorsal row and posteroventrally. Hind tibia similar, the dorsal rows with 7 or 8 tiny, slender bristles; middle and hind tibiae with strong spiculate ventral bristles. Claws slender only slightly curved with pulvilli long and slender.

Wings: Comparatively large, broad basally, hyaline on the outer half and posterior margin and similar in both sexes. The whole of the costal cell, auxiliary cell, base of marginal cell, whole of second and third basal cells light reddish brown. Also the basal part of the discal, fourth posterior, and anal cells and alula are tinged with reddish brown diffusely merging into the hyaline part of the wing. The marginal cell subapically is rather strongly widened backward, the second vein has a spoonlike loop. The posterior cells and the anal cell are all widely open. The anterior crossvein enters the discal cell at the middle. The second vein arises rectangularly with rounded bend distinctly basal to the anterior crossvein at least as much as the length of that crossvein. Ambient vein complete, alula relatively narrow, basal comb weak, the basal spur sharp but lappetlike.

Abdomen: Obconical with somewhat rounded sides in both sexes, the base as wide as the thorax, and the length approximately the same as the thorax. The color is chiefly light yellowish brown in the male, which has a wide, basal, black band over the middle of tergite, not reaching the apex of the sides, a smaller band on the third tergite and a medial spot on the fourth, likewise black. The female, however, is much more extensively blackish, only the sides of the tergites, the posterior margin of the fifth and the sixth and the whole of the seventh being reddish. There are 7 tergites observable in both sexes, the last one being comparatively long and more or less triangular. The pile of the abdomen is pale whitish yellow or cream-colored, forming a broad, wide brush of erect dense pile on the lateral third of the first tergite, continuing down the lateral margin of the abdomen, less dense, somewhat shorter and subappressed backward. Dorsum of the tergites with comparatively abundant similar pile, mostly flat-appressed, more abundant along the base of the margins and more likely to be denuded posteriorly. Female terminalia with about 4 or 5 quite slender, long, reddish, acanthophoric bristles or spines on each side. Male terminalia small rather

strongly recessed, quite ventral in position and tending to be obscured by overlapping pile.

Hesse states:

Of the hypopygium that the apical angles of the shell-like basal parts are slightly produced, bases of latter also produced and lobe-like; beaked apical points somewhat flattened from side to side, slightly twisted; aedeagal apparatus with the aedeagus itself very short and the ventral aedeagal process prominently projecting, its apical part flattened and broadened spoon-like, ending apically below in a recurved lip-like or ledge-like process which is usually not much evident or is depressed against the surface in dried specimens.

Material available for study: A pair of the type-species sent for study and dissection by the courtesy of Dr. A. J. Hesse of the South African Museum, Cape-town.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Synthesia fucoides* Bezzi, 1921.

Genus *Thyridanthrax* Osten Sacken

FIGURES 169, 171, 188, 217, 218, 220, 221, 705, 725, 958, 959

Thyridanthrax Osten Sacken, *Biologia Centrali-Americana*, Dipt., vol. 1, p. 123, 1886. Type of genus: *Anthrax selene* Osten Sacken, 1886. Designated by Coquillett, p. 615, 1910, the first of 4 species.

Ethyranthrax Becker, *Ann. Mus. Nat. Hungarici*, vol. 14, p. 44, 1916. Type of subgenus: *Anthrax vagans* Loew, 1862. See Bezzi, p. 7, 1924 for designation.

Tumulus, new subgenus. Type of subgenus: *Anthrax misellus* (Loew), 1869.

Oriellus, new subgenus. Type of subgenus: *Anthrax stigma* (Klug), 1832.

Bezzi (1924), pp. 193-195, key to 20 Ethiopian species.

Engel (1936), pp. 524-527, key to 33 species.

Austen (1937), pp. 147-148, key to 9 species from Palestine.

Hesse (1956b), p. 528, key to 55 male and 51 female species and subspecies.

Bowden (1964), pp. 101-102, key to 11 species from Ghana.

Medium-sized flies falling into several disparate groups, especially as far as the Palaearctic and Ethiopian species are concerned. The typical members of the genus are exemplified by the type-species, *selene* Osten Sacken; this and a number of other species from both the above regions, together with Nearctic species—I have at least 6 before me—have the wings dark at the base with characteristic hyaline spots centered about the crossveins and vein furcations. Some other characteristics of the restricted group *fenestratus* Fallen are: the end of the discal cell is pointed, not transverse; those species with windowlike spots strongly developed have a very short contact of the fourth posterior and discal cells; the abdomen has stiff, shaggy, appressed, bristly pile both dorsally and especially laterally and terminally. Within the genus the face varies from bluntly convex (slightly protuberant below) to obtusely conical, the peak quite short. The antennae are bulb-conical with the stylar portion slender and generally much shorter than in *Chrysanthrax* Osten Sacken.

In 1924, Bezzi widened the scope of the genus as far as Palaearctic and Ethiopian species are concerned to include several quite different groups. He recognized four groups. He included the clear-winged species that Becker (1916) had relegated to his *Exhyalanthrax* and who regarded them as a subgenus of *Villa* Loew. Still earlier Becker had placed *Thyridanthrax* Osten Sacken, as conceived by Osten Sacken, as a subgenus of *Hemipenthes* Loew; Paramonov (1927) adopted the same view. Bezzi in his broadening of the concept in 1924 included the group *afer* Fabricius, species with conical face and extensive, nonfenestrate wing pattern; this group and the clear-winged *Exhyalanthrax* Becker group include some parasites of *Glossina* Wiedemann flies among the South African member species.

Hesse (1936) notes that most authors have followed Bezzi in his broadened concept of *Thyridanthrax* Osten Sacken, but Hesse makes an excellent case for the restriction of *Thyridanthrax* Osten Sacken to the shaggy, fenestrate group of species, some of which are found in all three world regions cited above.

However, I feel that the old name *Exhyalanthrax* Becker may well be revived for the inclusion of those Old World species which have almost entirely hyaline wings. I, therefore, utilize it in a subgeneric capacity in this work. I also find it necessary to segregate species like *semifuscus* Engel and *misellus* Loew with their curious apically stout third antennal segments to separate status. For these I propose the subgenus *Tumulus*, with type *misellus* (Loew), 1869. I also cannot avoid the conclusion that the species *stigmulus* Klug and *vagans* Loew with their *Exoprosopa*-like articulated style should also be separated. For them I propose the subgenus *Oriellus*, with type *stigmulus* (Klug), 1832. I would agree with Hesse that much further subdivision of this large group of flies must be left for a time when some worker can attempt to elucidate large segments of the genus on a basic study of the genitalia of the Palaearctic and Nearctic species. Such a study might be attempted in the relatively near future, but it will be a long time before life histories can be added for more than a few species, since this type of study proceeds slowly and is often based upon fortuitous discoveries.

It is possible that the more conical-faced European species now in *Thyridanthrax* Osten Sacken, if critically studied, would fall into *Chrysanthrax* Osten Sacken. Painter (1933) separates these 2 primarily on the shape of the face.

It is perhaps not inappropriate to take note of the general similarity of some species of *Thyridanthrax* Osten Sacken to *Exoprosopa* Macquart. The *fenestratus* Fallen group has several species, such as *ternarius* Bezzi and *luctus* Loew, with 3 submarginal cells commonly and typically present; they are separable from *Exoprosopa* Macquart only by the lack of a third antennal segment, articulated style, and the absence of the characteristic tooth at the base of the claw. Some species of *Exoprosopa* Macquart, like *divisa* Coquillett, have a

strongly fenestrate wing pattern. Although Engel (1936) gave the type-species as *Anthrax fenestratus* Fallen, Coquillett (1910) had made a previous designation.

Species have been placed in this genus from Chile, and if *afer* Fabricius is included, it is recorded by Kertész from India and Oceania. Painter (1964) lists 9 Nearctic species. The majority are from southern Europe, Asia Minor, North and South Africa.

Length: 4 to 15 mm., most species 7 to 13 mm.

Head, lateral aspect: Head hemiglobular with very extensive occiput. The occipital pile consists of flat-appressed, loosely distributed scales and a quite short, dense fringe around the central cup or recess. The eye is reniform with a shallow, extensive indentation. From the lateral aspect the lower corners of the eye are rounded so that the eye bulges somewhat backward and the upper eye corners are rather strongly rounded. The facets at the lower corner of the eye are quite small, and there is only a slight enlargement of the facets on each side of the front. There is a short bisecting triangle at the bottom of the indentation and no bisecting line. The front is covered with abundant, coarse, erect pile, and some flat-appressed scales which become more dense on the face. While there are some fine hairs upon the face, they are scanty, and even the fringe which extends over the edge of the oral recess is scanty. The proboscis and labellum are slender, reaching slightly beyond the apex of the oral recess. The palpus is cylindrical and not quite half as long as the proboscis. It has only very fine hairs fringing it ventrally and laterally. The antenna is attached at the upper third of the head. The first segment is swollen apically and sometimes medially. The first antennal segment bears considerable, rather long bristly pile, not longer than this segment. Second segment small and bead-shaped. The third is elongate conical, the short pile becoming quite slender and bearing a minute bristle.

Head, anterior aspect: As wide as the thorax, nearly circular from the front, but slightly flattened above and on the sides. The genae extend down below the eye rather conspicuously, though not more than the thickness of the proboscis, yet more so than in related genera. The antennae are widely separated, distant from the eye margin by rather less than the first antennal segment. The oral recess is chiefly ventral, but slightly oblique, narrow, deep posteriorly with vertical sides, and strongly narrowed anteriorly toward the apex of the face where the sides are somewhat widened or obliquely sloping inward. From above, the lobes of the occiput are tightly apposed, rather horizontal in position, but with a neat, deep, narrow, cleftlike fissure behind the ocelli. The ocellar tubercle is a little elongate, quite prominent and protrusive, yet not rising above the uppermost level of the eye. In males the eyes are rather narrowly separated by not more than and sometimes less than the width of the ocellar tubercle.

Thorax: The thorax is broad anteriorly, at least as wide anteriorly as the mesonotum is behind the wing,

but the mesonotum is a little wider across the postalar callosities. The ground color is black with faint, dark brown pollen, and the scutellum may be almost entirely reddish or yellow in some species, or the basal half may be black. Pile of the mesonotum consists of fine, appressed, bristly or scaliform hair with considerable amounts of erect or suberect, stiff, pale pile, becoming more dense, anteriorly, and merging into an anterior collar which may be extensive, and which may form a wide, broad band along the anterior margin. In other species there is no progressive gradation of this anterior pile into the remainder of the mesonotum. The propleuron and mesopleuron are extensively pilose with tufts of very coarse pile. There are few hairs on the pteropleuron. The metapleuron is densely and widely pilose. There is a tuft of hair beneath the haltere, and a conspicuous tuft appressed downward above the posterior coxa. The anterior hypopleuron is bare, but the plumula bears much long pile and the scales of the squama and alula are long and conspicuous and extend as shorter scales onto the axillary lobe.

Legs: Anterior pair of legs much reduced, the anterior tibia smooth. The tarsus is small and the claws minute. The middle femur bears anteroventrally a fringe of long, slender bristles, 5 to 7 in number. Hind femur with 5 to 12 slender, oblique bristles, a little more stout in some species, and a few short bristles of spicules dorsally at the apex. All the femora, especially the hind femora, and the last four tibiae with conspicuous, narrow, appressed scales. Middle and posterior tibiae with numerous, fine, oblique bristles in 4 rows, and some shorter setae intermixed. Most of these rows have 10 such bristles, but the anterodorsal row on the hind tibia of *nugator* Coquillett has more than 20 such bristles. Claws small, quite slender, sharp, and scarcely curved. Pulvilli absent.

Wings: The wings tend to be broad at the base and pointed apically. Characteristically they have rather more than the basal half diagonally colored with brown or brownish black of varying intensity. Always with irregular margin and sometimes diffuse. This basic black basal color in a few species is reduced to a series of diffuse spots. But in those species with a more intense pattern of brown, very characteristically there are windowlike spots, one extending on the anterior crossvein and above it, one extending on all four sides of the contact point of the discal and fourth posterior cell. Another on all sides at the upper end of the second basal cell and generally at the base of basal cells. The anterior crossvein enters the discal cell at the middle or often distinctly beyond the middle, though never as far as the outer third. In some of the European species, placed by European authors in this genus, the anterior crossvein may be relatively basal, even located at the basal third of the discal cell; and at least 4 or 5 European species lack the windowlike spots and have only a pale fleck within the brown area located where the thyridium is normally placed. It is notable that these European species that lack the fenestrate wing likewise

have a long contact of the discal cell with the first posterior, and the typical species of the genus show a tendency for the contact of discal and posterior cells to be either punctiform or at least short.

The type-species of this genus is *selene* Osten Sacken and not *fenestratus* Fallén as given by Engel. The shape of the discal cell varies widely, sometimes long, sometimes quite short. The first posterior cell is a little narrowed, the anal cell widely open, the alula about 3 times as long as wide, and there are only 2 submarginal cells. The ambient vein is complete. Another interesting character lies in the extraordinary width of the costal comb. The costal hook is long and thornlike.

Abdomen: The abdomen is short oval, mostly black in ground color, but some species at the sides of the basal tergite and the last two tergites are more or less brownish yellow, or with reddish brown that extends inward toward the midline. The pile is dense and consists of slender matted scales or scaliform pile, sometimes with bands of varying color along the posterior margins, and often in many species with a considerable amount of fine, erect, or suberect pile which may form a bristly terminal fringe. Males may have a little silvery pile on the last tergite. Females with the terminalia recessed and bearing several pairs of spines on the lateral margin of the acanthophorite. Male terminalia comparatively large but recessed and asymmetrical, enclosed by the last sternite which pinches together to form a protecting cover.

Dr. A. J. Hesse was able to study a very large assemblage of species in this genus; for this reason I quote his comments on the male genitalia:

Hypopygium of males usually with a dorsal ridge on each shell-like or clasper-like basal part, this ridge usually hairy, usually projecting freely in the form of a short process posteriorly, the freely projecting part sometimes fused with its neighbour, forming a U-shaped crest on the two basal parts; aedeagus proper usually short, sinuous; aedeagal apparatus always with a conspicuous, projecting, scoop-like, aedeagal process which differs in shape in the various species and is usually provided apically and ventrally on each side with a hooklet or spine.

The male terminalia from dorsal aspect, epandrium removed, show a remarkably broad, wide, long, extensive epiphallus, quite tongue-like. The basal part of the aedeagus short oval and egg-shaped. In the lateral aspect, the dististyle is apical with dorsoapical incision and hook. The ejaculatory duct is separated below from the epiphallus. The epandrium has a strong basal, downward lobe, leaving a wide ventroapical incision, much as in *Rhynchanthrax* Painter.

Material available for study. All the material in the National Museum of Natural History, the Museum of Comparative Zoology at Harvard, the British Museum (Natural History), and considerable personally collected material.

Immature stages: The larvae of these flies consume pods of locust eggs; they also parasitize *Glossina* and *Calliphora*.

Ecology and behavior of adults: The adults are abundant on many types of low-growing flowers, especially composites.

Distribution: Nearctic: *Thyridanthrax atratus* (Coquillett), 1887 (as *Anthrax*); *bifenestratus* (Bigot), 1892 (as *Anthrax*); *fenestratoides* Coquillett, 1892 (as *Anthrax*) [= *macula* (Cole), 1919 (as *Anthrax*)]; *melasoma* (Wulp), 1882 (as *Anthrax*); *nugator* (Coquillett), 1887 (as *Anthrax*); *pallidus* (Coquillett), 1887 (as *Anthrax*); *pertusus* (Loew), 1869 (as *Anthrax*); *sylene* (Osten Sacken), 1886 (as *Anthrax*) [= *otiosa* (Coquillett), 1887 (as *Anthrax*)]; *utahensis* Manghan, 1935.

Neotropical: *Thyridanthrax hypoxanthus* Macquart, 1840 [= *blanchardii* (Philippi), 1865 (as *Anthrax*)]; *semilugens* Philippi, 1865 [= *unicinctus* (Bigot), 1892 (as *Anthrax*)]; *semitristis* Philippi, 1865.

Palearctic: *Thyridanthrax afer* (Fabricius), 1794 (as *Anthrax*), [= *fimbriatus* (Meigen), 1804 (as *Anthrax*)], = *sirius* (Hoffmannsegg in coll. in Meigen), 1820 (as *Anthrax*); *agnitionalis* Austen, 1937; *albicingula* Austen, 1936; *albinus* Becker, 1913; *albosegmentatus* Engel, 1936; *amoenus* Austen, 1937; *angusteculatus* (Becker), 1902 (as *Anthrax*); *anus* (Wiedemann), 1828 (as *Anthrax*); *argentifer* (Becker), 1916 (as *Exhyalanthrax*); *autumnalis* (Becker), 1916 (as *Exhyalanthrax*); *chinophorus* Bezzi, 1925; *circe* (Klug), 1832 (as *Anthrax*); *daguiensis* Paramonov, 1934; *elegans* (Wiedemann in Meigen), 1820 (as *Anthrax*), [= *variegatus* Jaenicke, 1867]; *fenestratus* (Fallen), 1814 (as *Anthrax*), [= *fenestralis* Wahlgren, 1907, = *nigrilus* (Fabricius), 1781 (as *Bibia*)], = *ornatus* (Curtis), 1824 (as *Anthrax*), = *variegatus* (Pallas in Wiedemann), 1818 (as *Anthrax*); *fenestratus montanus* Paramonov, 1926; *fulvifacies* Austen, 1937; *gracilis* Paramonov, 1926; *griseolus* (Klug), 1832 (as *Anthrax*); *heteropterus* Paramonov, 1926; *hispanus* (Loew), 1869 (as *Anthrax*); *inauratus* (Klug), 1832 (as *Anthrax*); *incanus* (Klug), 1832 (as *Anthrax*) [= *testaceus* (Macquart), 1840 (as *Anthrax*)]; *indigenus* Becker, 1908 (as *Anthrax*); *innocens* Austen, 1936; *intermedius* (Paramonov), 1927 (as *Hemipenthes*); *irrorellus* (Klug), 1832 (as *Anthrax*) [= *inconspicuus* (Loew), 1856 (as *Anthrax*)]; *kushkaensis* (Paramonov), 1927 (as *Hemipenthes*); *latipennis* Paramonov, 1927; *latona* (Wiedemann), 1828 (as *Anthrax*); *lepidulus* Austen, 1937; *leucotaeniatus* Engle, 1936; *lineus* (Loew), 1860 (as *Anthrax*); *lotus* (Loew), 1869 (as *Anthrax*) [= *confusus* Becker, 19—]; *mucrops* (Portschinsky), 1887 (as *Anthrax*); *melanchlaenus* (Loew), 1869 (as *Anthrax*); *mervensis* Paramonov, 1926; *minutus* (Macquart), 1849 (as *Anthrax*); *miscellus* (Loew), 1869 (as *Anthrax*); *montanorum* Austen, 1936; *mutilus* (Loew), 1869 (as *Anthrax*); *nebulosus* (Dufour), 1852 (as *Anthrax*) [= *nubilus* Loew, 1871, lapsus, = *occipitalis* Loew, 1869]; *nitidifrons* Austen, 1936; *noscibilis* Austen, 1936; *obliteratus* (Loew), 1862 (as *Anthrax*); *pauper* Becker, 1916 (as *Exhyalanthrax*); *perspicillatus* Austen, 1937; *perspicillaris* (Loew), 1869 (as *Anthrax*)

[= *fenestratus* (Meigen), 1820 (as *Anthrax*)], = *gallus* (Loew), 1869 (as *Anthrax*); *polyphemus* (Wiedemann in Meigen), 1820 (as *Anthrax*), *polyphemus pumilio* Austen, 1937; *punctum* (Loew), 1869 (as *Anthrax*); *rohdendorfi* (Paramonov), 1925 (as *Villa*); *rotundifacies* Paramonov, 1926; *rubriventris* Paramonov, 1926; *samarkandicus* Paramonov, 1926; *semifuscus* Engel, 1936; *stimulus* (Klug), 1832 (as *Anthrax*); *tabaninus* Bezzi, 1925; *timurensis* Paramonov, 1926; *transcaspicus* (Paramonov), 1924 (as *Exhyalanthrax*); *turcomanus* Paramonov, 1926; *unctus* Loew, 1869; *unicolor* (Becker), 1902 (as *Anthrax*); *vagans* (Loew), 1869 (as *Anthrax*) [= *marginalis* Loew, 1869], *vagans beckeri* (Paramonov), 1926 (as *Hemipenthes*), *vagans contrarius* (Becker), 1916 (as *Exhyalanthrax*), *vagans parvus* (Paramonov), 1926 (as *Hemipenthes*), *vagans unistriatus*, Engel, 1936; *venustus* Austen, 1936; *vetulus* (Wiedemann), 1828 (as *Anthrax*).

Ethiopian: *Thyridanthrax aberrans* Hesse, 1956; *abruptoides* Hesse, 1956; *abruptus* (Loew), 1860 (as *Anthrax*); *alliopterus* Hesse, 1956; *anisospilus* Hesse, 1956; *arenicolus* Hesse, 1956; *argentifrons* Austen, 1929; *argyrolophus* Hesse, 1956; *atricentris* Hesse, 1956; *bechuanus* Hesse, 1956; *beckerianus* Bezzi, 1924; *beneficus* Austen, 1929; *bolboceus* Hesse, 1956; *brevifacies* Hesse, 1956; *burtii* Hesse, 1956; *caffariae* Hesse, 1956; *calochromatus* Bezzi, 1921; *cidarellus* Hesse, 1956; *griseifrons* Hesse, 1956; *idolus* Hesse, 1956; *incipiens* Bezzi, 1924; *lugens* (Loew), 1860 (as *Anthrax*); *luteolus* Bezzi, 1924; *lutulentus* Bezzi, 1921; *macquarti* Bezzi, 1912; *melanopleurus* Bezzi, 1912; *monticolus* Hesse, 1956; *nitidifrons* Hesse, 1956; *niveifrons* Hesse, 1956; *occidus* Hesse, 1956; *phileremus* Hesse, 1956; *pseudoflammiger* Bezzi, 1924; *salutaris* Austen, 1929; *semilautus* Hesse, 1956; *simmondsi* Hesse, 1956; *stylicornis* Hesse, 1956; *subperspicillaris* Bezzi, 1924; *ternarius* Bezzi, 1921; *ternarius speciosus* Hesse, 1956; *thyridus* Hesse, 1956; *transiens* Bezzi, 1921; *triangularis* Bezzi, 1924; *urogatus* Hesse, 1956; *vicinalis* Hesse, 1956; *zinnii* Hesse, 1956.

Oriental: *Thyridanthrax uncinatus* Guérin, 1838.

Genus *Rhynchantrax* Painter

FIGURES 232, 401, 716, 727, 964, 965

Rhynchantrax Painter, Journ. Kansas Ent. Soc. vol. 6, p. 6, 1933a. Type of genus: *Anthrax parvicornis* Loew, 1869, by original designation.

Painter (1933), p. 7, key to 5 species.

Small to medium-sized flies with approximately the basal half of the wing dark brown but sharply and irregularly and diagonally delimited and enclosing paler windowlike spots. From other genera of the *Villa* Lioy complex it is separated by the sharply narrowed bulblike base of the third antennal segment with its very long, slender style. In the long, slender style and in the long, slender proboscis and labellum, which is about twice as long as the head, it is quite similar to

Lepidanthrax Osten Sacken; from it separated by the broad wing, different type of wing pattern, and the absence of the patches of matted scales on the sides of the abdomen. In *Rhynchanthrax* Painter the bristles of the anterior tibia vary even within the species; I have individuals of *parvicornis* Loew from Kansas with strong, stout bristles, others from Mississippi with weak, fine bristles. Pulvilli are absent; this character and the 2 submarginal cells separate these flies from *Stonyx* Osten Sacken.

The range of this genus extends from Colorado, Kansas, and Illinois on the north to Mississippi on the east, Arizona on the west, and Texas and northern Mexico on the south.

Length: 5 to 14 mm.

Head, lateral aspect: Head is hemiglobular, but the occiput is only moderately produced and developed backward and the occipital pile is appressed, short and bristly with rather narrow scales, the central fringe short. The indentation of the eye is unusually shallow, although the occiput is extensive above and below, and the eye facets at this point curve forward leaving a small triangular indentation, but no bisecting line. The front has much apparently short, fine, erect, bristly hair, some faint pollen and numerous flat-appressed scales especially on the anterior half. Occasionally they are reduced in quantity, becoming more numerous, though loose and scattered in appearance on the face. Characteristically the face has a considerable amount of fine, erect, or suberect bristly pile, in length scarcely longer than the second antennal segment. The face may be described as bluntly extended forward, maximum length from eye being slightly more than the length of the three antennal segments if the style be excepted. The face is not peaked or conical but blunt anteriorly.

The proboscis in this genus is very slender, the labellum also, and it is characteristically elongate, extending far beyond the apex of the oral recess. It is nearly twice as long as the oral recess. Palpus very slender and cylindrical with fringe of stiff, bristly hairs ventrally and laterally. The antenna is attached near or just below the upper third of the face and all the segments of the antenna are small, the first segment scarcely longer than wide with a few short bristly hairs on all sides, except below. Second segment beadlike, a little wider apically, broadly attached to the base of the third antennal segment. The third segment is a quite small onion-shaped or bulb-shaped segment and short with an abruptly formed, very slender style of considerable length. The whole segment is very much like that of *Lepidanthrax* Osten Sacken which, incidentally, also has a long proboscis. The style of the antenna is a little longer than the total length of the three segments.

Head, anterior aspect: The head is large, as wide as the thorax. The eyes are rather widely separated, even in males, by 3 times the width of the ocellar tubercle and by at least the length of the three antennal segments. In the female it is at least 4 times as wide as

the ocellar tubercle. The antennae are unusually widely spaced apart, the space from the eye margin is rather less than the length of the first segment. The oral recess is wider than in related genera, deep posteriorly, and narrowed only quite near the anterior peak or face, and this narrowed area is widened by obliquely sloping inward. The palpus is unusually long and filiform and the proboscis has a double bulbiform base. Viewed from above the ocellar tubercle is rather low, but placed distinctly forward from the anterior corners of the eye, which are broadly rounded. Lobes of the occiput are vertical and not touching.

Thorax: the thorax is subquadrate, widened only across the prominent postalar callosities. It is black with dark brown pollen, the apical half of the scutellum more or less obscurely reddish brown. The pile of the mesonotum is coarse, short and appressed or subappressed. There is a row of very fine, erect hairs in front of the scutellum. The anterior marginal band of pile is coarse, wide in depth, and the pile comparatively short. There are 3 or 4 bristles on the notopleuron, some bristly pile anterior to these, 4 or 5 longer bristles on the postalar callosity and 7 or 8 pairs on the margin of the scutellum which are long and conspicuous. Propleuron and mesopleuron with extensive, long, coarse, dense, appressed pile. There are a few hairs on the pteropleuron. The metapleuron has dense pile, but the hypopleuron is bare anteriorly and posteriorly. There is a tuft of hair beneath the haltere and the plumula is densely pilose. Squamal scales are conspicuous and other long, extending onto the alula and the axillary lobe.

Legs: The legs are stout, including the anterior pair which are well developed. The anterior pair has only the tarsus reduced and with a fringe of fine hair rather than setae. The front tarsal claws are rather large. The middle femur has several stout bristles placed in the middle anteriorly. The hind femur has 8 to 10 bristles anteroventrally; in some species it is slender, in other species stout. Characteristically the anterior tibia is spiculate in several rows, but these bristles are fine, evident but not conspicuous. Hind tibia with 4 rows of bristles, moderately long and oblique. There are 7 or 8 anteroventral, 10 to 14 anterodorsally, including the smaller setae and rather small finer bristles in the other two rows. Claws stout, not very long, and pulvilli quite rudimentary or absent.

Wings: Broad at the base, pointed apically, the basal half of the wing is diagonally covered with dark sepia brown, the margin sharp, but irregular and with fenestrate spots at and above the anterior crossvein at the end of the second basal cell and below it and likewise narrowly at the base of the basal cells. The depigmented fleck on the thyridial area is large. The first posterior cell is scarcely narrowed, the anal cell is widely open. There are only 2 submarginal cells. The alula is 3 times as long as wide. The ambient vein is complete and fringed, and the costal comb while not as conspicuous as in *Thyridanthrax* is wide and has many stout setae, and the costal hook is sharp and strongly thornlike.

Abdomen: Short and obtuse, wider than the thorax, black in some species, reddish orange in others with medial black bands on the second and third and fourth tergites of decreasing width, but the first tergite is always entirely black. The pile consists of dense, appressed scales for the most part, which are black and yellow or intermixed, and which laterally in *texana* Painter are orange red. Viewed laterally a few fine, black hairs are suberect, and these become more in evidence laterally and on the last two tergites. Sides of first two tergites with copious long, dense, pale, coarse pile. The acanthophorites have a row of spines on the side. The male terminalia are large and asymmetrical and rather strongly recessed.

The male terminalia from dorsal aspect, epandrium removed, show a very wide, long, apically rounded epiphallus with nearly parallel sides. The basal part of the aedeagus is large and short oval, the lateral apodemes are paired. From the lateral aspect the dististyle is thick, only moderately long, with dorsoapical incision and hook. The epiphallus is long and thick without distinctly separated ejaculatory process. The epandrium is much rounded, especially basally or posteriorly. It has a deep, wide, anterior incision on the lower half.

Material available for study: A series of the type-species and one more species; also, the series in the National Museum of Natural History.

Immature stages: Parasites of white grubs. See life histories.

Ecology and behavior of adults: These flies are not uncommon on a variety of flowers and are especially attracted to *Rudbeckia* species and other composites.

Distribution: Nearctic: *Rhynchanthrax parvicornis* (Loew), 1869 (as *Anthrax*); *quivera* Painter, 1933; *rex* (Osten Sacken), 1886 (as *Anthrax*) [= *plagosa* (Coquillett), 1887 (as *Anthrax*)]; *texanus* Painter, 1933.

Genus *Paranthracina* Paramonov

Paranthrax Paramonov, Trav. Mus. Zool., Kieff, no. 11, p. 57, 1931. Type of genus: *Paranthrax africanus* Paramonov, 1931, by monotypy. Preoccupied Bigot, Bombyliidae, 1876.

Paranthracina Paramonov, Trav. Mus. Zool. Kieff, no. 12, p. 52, 1933. Change of name.

I have not been able to see this genus.

Distribution: Ethiopian: *Paranthracina africanus* Paramonov.

Genus *Villoestrus* Paramonov

FIGURES 410, 682, 685

Villoestrus Paramonov, Trav. Mus. Zool. Kieff, no. 11, p. 93, 1931. Type of genus: *Villoestrus uvarovi* Paramonov, 1931, by original designation.

Large, robust, broad, very compact, obtuse, greasy flies in which the oragenal cavity is reduced to a mere slit or narrow cleft. The proboscis and palpus are completely absent. Related to *Oestranthrax* Bezzi and sev-

eral other Exoprosopinae with reduced mouthparts, they represent a much more extreme specialization. The head is large, subglobular and together with face and front, it is very strongly convex. There are some other peculiarities. The auxiliary vein extends far toward the wing apex. There appears to be a vena spuria immediately behind the first vein. There are 2 submarginal cells and the 4 posterior cells are widely open. The discal cell is shaped like a shoe or slipper and the anterior crossvein enters at the middle; the second vein arises almost rectangularly just in front of the anterior crossvein. The anal cell is closed with a short stalk. Wings sometimes strikingly dimorphic in color and pattern; males may have a strong brownish blotch across the middle or lack it; female of *dimorphus* Hesse has a very dark, conspicuous anteromedial blackish spot on the wing; female of type-species unknown. The abdomen is especially thick and high. The general color varies from pale ochraceous brown to reddish.

These rare flies are known from Palestine and from Strandfontein dunes in the Cape Flats near Capetown, South Africa.

Length: 16 to 16.5 mm., in both species; wing 12 to 13.5 mm.

Head, lateral aspect: The face is rather prominent but strongly convex and receding; it ends below in a deep, narrow, oblique crease or fissure which does not quite extend to the middle of the face. Just before its medial end, which is deep punctate, it extends shallowly and longitudinally a short distance back toward the occiput. The cheeks are wide but do not extend below the eye, except for a faintly linear margin; they are barely visible at the bottom of the eye. The oral opening is confined to a short, narrow cleft or slit; proboscis and palpus absent. The eye is much longer dorsally, therefore only gently convex above but strongly convex below; the posterior margin in the middle has a low indentation and a long continued transverse crease upon the eye. The occiput is thick and prominent but gently sloping medially and with a very large, abrupt, deep, central concavity; the pile of the occiput is extremely scanty, minute, fine, and laterally flat-appressed; upper occiput without a dorsal fissure. The antennae are attached at the middle of the head and short; the first segment is as long as the second and third with the style omitted. This first segment is greatly swollen along its medial aspect and is therefore much wider than the second, the second segment is quite short and disclike; the third segment is curiously and rather strongly compressed, flattened on the outer surface; it is convex medially, pyriform, the style narrow, slightly longer than the segment itself, very slightly dilated at its apex and with a minute conical spine.

Head, anterior aspect: The face bears dense, stout, stiff, subappressed pile with black and yellow hair intermixed; the latter is somewhat flattened or scalelike and with distinct rather broad scales on the upper half between the antennae and on the front. Antennae separated by a distance nearly equal to the combined length

of all three segments, style omitted. The front also has considerable short, suberect, coarse, black pile. The ocellar triangle is small, low, nearly equilateral, the ocelli small.

Thorax: Rather densely short, matted, fine pilose; especially matted with pale pile along the lateral margins, much of the mesonotum is bare; this is almost certainly due to being denuded. Scutellum large, wide, rather convex and somewhat gently swollen over the middle and abrupt at the base, with densely tufted, matted, fine, pale pile laterally and along the margin and with shorter appressed pile of the same color on the disc. There is scarcely any trace of anteromedial depression marking off the large swollen postalar callosity. Pleuron with a dense tuft of pile of rather fine pale color anteriorly below or on the anterior margin of the humerus and across the anterior margin forming a collar; also over almost the whole of the mesopleuron and with an especially dense tuft on the metapleuron. Sternopleuron with abundant but less dense pile, a scanty tuft on the pteropleuron and the posthypopleuron; lateral metanotum pilose.

Legs: Small, short and weak with small, fine scales on the femur and tibia; there is no long pile. It has minute fine setae on the hind femur, more numerous fine, short bristly hairs on the anterior femur; the hind tibia has a lateral, ventrolateral, dorsolateral and dorsomedial row, medial row and ventromedial row of fine, short setae or minute bristles; anterior femur with 2 rows posteriorly and 1 dorsal or posterodorsal row.

Wings: Slightly reduced in size, and relatively short, but strong and broad. Mostly hyaline, they may differ in color within the sexes and in some females have a strong central black pattern. The basal costal hook is stronger than in *Oestranthrax* Bezzi and broader. The second vein has no basal stump, and is not as sharply curved upward apically and, moreover, the second submarginal cell is longer; also, the second and third posterior cells are decidedly longer; the discal cell is shaped like a shoe or slipper and is somewhat constricted in the middle; the anterior crossvein enters at the middle and the second vein arises just basal to it and arises abruptly. The axillary lobe is broader, the alula wide, the ambient vein complete.

Abdomen: Short, thick, obtuse, with a dense tuft of more or less erect, fine, brownish-white pile laterally on the first segment and equally dense, flat-appressed, matted pile laterally on the second and the third tergites; on the third tergite most of this pile becomes small, slender scales; the third and the very short fourth, fifth, sixth, and seventh tergites and their sternites have rather numerous, slender, brownish-yellow scales. There are visible from above 7 tergites in the male with a short eighth tergite concealed beneath the seventh. Terminalia quite short and inconspicuous.

Material available for study: The type-species in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Unknown. Hesse (1956) remarks that the South African species was overlooked by dipterists and captured by a lepidopterist looking for butterflies! He comments on the "short seasonal occurrence" this genus must have.

Distribution: Palaearctic: *Villoestrus uvarovi* Paramonov, 1931.

Ethiopian: *Villoestrus dimorphus* Hesse, 1956.

Genus *Oestranthrax* Bezzi

FIGURES 166, 230, 233, 394, 683, 686, 740, 775, 783, 955, 956, 957

Oestranthrax Bezzi, Ann. South African Mus., vol. 18, p. 130, 1921. Type of genus: *Anthrax obesus* Loew, 1863, by original designation; first mentioned here. Described in: Voyage Alluaud et Jeannel Afrique orientale, pt. 6, p. 326, 1923.

Engel (1936), pp. 556-561, descriptions of 4 species, 2 subspecies, Palaearctic.

Hesse (1956), pp. 511-512, key to 4 South African species.

Strange flies of large size, and rather obese and bloated form. This fly is unique because of the much reduced mouthparts; the mouth opening itself is small and the proboscis is rudimentary; cheeks broad and separated from the face region by a deep fissure or furrow. Palpus short and distinct. No macrochaetae on thorax. Wings shorter than the body of fly and the second basal cell is short and dilated. Wings hyaline. Bezzi (1924) relates this fly to the *Villa* Liroy complex of genera, and notes a similar trend toward reduction of mouthparts in such flies as oestrids, the tabanid *Adersia* Austen, and the muscoids of the group *Trixinae*; he correlates the reduction with high degree of specialization in its parasitic relationship.

Oestranthrax Bezzi is related to *Villoestrus* Paramonov, which has complete reduction of mouthparts and loss of palpus, and *Marleyimyia* Hesse, intermediate between the other two genera. Hesse (1956) comments upon the peculiar oily exudate that comes from the surface of all these genera and suggests that the host of these flies is probably excessively rich in fats and oils. Could they be hyperparasites upon late stages of meloids? Related genera have been reared from logs containing *Cossidae*.

Oestranthrax Bezzi contains 8 species from Asia Minor and South Africa; there are also recently discovered species in Utah, U.S.A.

Length: 9.5 to 16 mm.; wing 8 to 14 mm.

Head, lateral aspect: The head is subglobose, the face moderately projecting, extensive, and of considerable depth but broadly rounded and retreating. Only the lower third of the front extends beyond the eye. The eye itself rather short and consequently much higher than long, the face is rather densely covered with conspicuous, more or less appressed or suberect, broad, pale scales extending nearly to the eye margin. The occiput is rather prominent and tumid, bilobate above with slender fissure and large, central, cuplike cavity. Pile of occiput scanty, fine, short, erect and located on the inner border around the cavity, except that the remain-

ing outer portion tends to have flat-appressed, matted, slender scales becoming dense at the eye margin. Posterior eye margin broadly and shallowly indented and with a bisecting crease in the middle. Pile of the front moderately abundant and consisting of slender, erect scales which are apt to be black, changing over to appressed yellow scales in front along the eye margin and also with a number of scattered, quite fine, erect, delicate, black hairs no longer than the scales and present throughout. The proboscis is very greatly reduced and vestigial and is snugly recessed within the small, shallow, oral cavity lying between the posterior eye corners. The palpus is present and short and appears to consist of 2 segments with the basal segment minute. It also is more or less recessed and lies on each side of the proboscis. The genae are moderately wide, although the oragenal space is narrowed across the proboscis.

The genofacial fissure is conspicuously deep and rather flared, overlapped by pile from the face. There is no oragenal cup in the usual accepted sense. Antennae attached slightly above the middle of the head. All antennal segments short, the first is about twice as long as the second, narrow at the base, and expanded somewhat ventrally at the apex. Second segment a little compressed and attached obliquely to the first segment. First segment with a tuft of long, coarse setae dorsolaterally and another one ventrally, third segment consists of a minute basal, bulblike portion abruptly followed by a slender, stylelike process, which is about as long as the first two segments together.

Head, anterior aspect: The head, no wider than the thorax or a little more narrow. The vertex of the female is narrow, approximately one-fourth of the width across the antenna. Ocellar tubercle quite small but with vertical sides and sharply demarcated. The ocelli are large, the anterior ocellus quite vertical, the others less so. They occupy a short isosceles triangle and the tubercle bears 2 or 3 setae of no great length. The antennae are widely separated at the base by a distance nearly equal to twice the length of the first segment.

Thorax: The thorax is broad and short, shallowly convex, the mesonotum feebly shining, rather densely covered with quite slender, appressed scales apt to be denuded across the middle but more in evidence as a band in front of the scutellum, or scattered along the anterior portion. Anterior margin of mesonotum with a moderately dense, not very long collar or band of erect, coarse, bristly, pale pile. Bristles are quite absent, the notopleuron has a dense, bushy tuft of extensive, erect, more or less radiating pile in front of the wing, and there is a narrow fringe or erect pile above the wing. Scutellum more or less triangular, wide at the base, the posterolateral angles broader than the anterobasal angle. Surface covered with scales and a few fine hairs along the margin. Squama with a fringe of dense, long hairs barely flattened. Mesopleuron with a very strongly developed, quite broad, dense, radiating tuft of pile below the haltere, another tuft lower down on the lateral metasternum. Hypopleuron bare.

Legs: The legs are rather short, all the femora a little thickened, the anterior tibiae and tarsi quite short, the former arcuate. Pile of the femora and tibiae consists entirely of appressed scales, the middle femur lacks any posterior fringe. Hind femur with 2 or 3 small setae below and a few still smaller setae laterally. All of the tibiae have conspicuous, quite fine, sharp spicules. They are comparatively well developed though of no great length or thickness. The anterior tibia has 4 rows of spicules about equally developed each with some 8 or 10 in number; it is slightly curved, with a fine brush of hair below. Spicules of hind tibia very little if any larger except ventrally. There are 5 rows that have 8 to 17 elements. Claws long and slender without basal teeth, curved from the base. Pulvilli absent.

Wings: The wings are hyaline, comparatively small, the costal cell and to some extent the first basal cell tinged with yellowish brown. Auxiliary vein ends obliquely but comparatively close to the end of the first vein. There are only 2 submarginal cells, but the anterior branch of the third vein has rather characteristic pattern being perhaps a little bit more abrupt in its origin and broadly rounded as it turns to the apex. Second vein arises a little before the anterior crossvein but rectangularly and without spur. The anterior crossvein enters the discal cell near or just beyond the middle. The upper vein of the third posterior cell has a shallow, angulate bend with a spur directed proximally in the discal cell. The discal cell is convexly widened both anteriorly and posteriorly; second basal cell quite short and wide. The alula is moderately large bearing a fringe of narrow scales; ambient vein complete. The base of the costa is expanded with prominent comb and a sharp basal spur.

Abdomen: The abdomen is very short oval, distinctly broader on the first three tergites than the thorax and covered densely with appressed scales, tending to be pale basally on the tergites and black posteriorly; first tergite, however, with dense, erect hairs, except along its posterior margin where the hairs are replaced by appressed scales.

The dististyli of the male are compressed laterally, rather twisted, and bifid as in *Villa* Lioy. The aedeagus is relatively short and according to Hesse (1956) has a well-developed scooplike process of which the central, dorsal, apical part is raised keel-like. The lateral struts project straight outward, the basal strut does not project beyond the base.

Since Dr. A. J. Hesse was able to base his conclusions upon a greater number of species, I quote his remarks upon the male hypopygium:

Hypopygium of male very much like that of *Villa*, especially of the *leucochila*-section; beaked apical joints compressed apically, more or less twisted, bifid apically as in *Villa*; aedeagal apparatus with a relatively short aedeagus and a well-developed scoop-like aedeagal process of which the central, dorsal, apical part is raised keel-like; lateral struts projecting straight out laterally; basal strut not projecting beyond bases of basal parts.

The male terminalia from dorsal aspect, epandrium removed, show a basally wide, apically narrowed, elon-

gate structure in which the epiphallus is very large, wide, apically widened and dilated, with apex rounded, and quite tongue-like in appearance. The basal part of the aedeagus is rather large, egg-shaped or bulblike. From the dorsal aspect the ramus proceeds backward as 2 long, curved, convergent, lobelike extensions extending as far backward as the end of the basal ejaculatory apodeme. From the lateral aspect, the epandrium is large and triangular, the basistylus large, stout or robust both apically and even more so above the base. The dististyli are short, stubby, dorsoapically incised and hooked and subapical in position. The epiphallus from lateral aspect is large, long, and tongue-like.

Material available for study: I am deeply indebted to Dr. A. J. Hesse of the South African Museum, Cape Town, for sending a pair of the type-species for dissection and study. I have also previously seen the species in the British Museum (Natural History), and I have seen the species *farinosus* Johnson and Maughan in the National Museum of Natural History.

Immature stages: Unknown.

Ecology and behavior of adults: Johnson and Maughan (1953) write of the fly *farinosus* Johnson and Maughan; this species inhabits the eastern edge of the Pahvant Valley of Utah, a broken terrain with intermittent areas of sand and loam and dominant vegetation sagebrush and greasewood, and they stated further that the sandy areas produced many kinds of bee flies, the loamy areas nearly barren yet it was in these more or less barren areas the flies of this genus were found. They were nearly always resting near the ground on dead twigs or stems, their pale color blending well with the weather-whitened wood; most of his 13 specimens were seen by walking into the sun and watching for the glint of sunlight on the heads and the epaulets of white scales on the wings; capture was difficult and uncertain, their darting flight being extremely rapid. They often returned to the same general locality, had to be captured in flight and were very easily abraded; a year later the same locality produced none.

Distribution: Nearctic: *Oestranthrax farinosus* Johnson and Maughan, 1953.

Palearctic: *Oestranthrax arabicus* Paramonov, 1931; *brunnescens* (Loew), 1857 (as *Anthrax*); *goliath* Oldroyd, 1951; *karavajevi* Paramonov, 1931; *rubriventris* Paramonov, 1934 (1936).

Ethiopian: *Oestranthrax disparilis* Hesse, 1956; *obesus* (Loew), 1863 (as *Anthrax*), *obesus olferi* Paramonov, 1931, *obesus pallifrons* Bezzi, 1926; *speiserianus* Bezzi, 1923; *ziminii* Paramonov, 1934 (1936).

Oestrimyza, new genus

FIGURES 415, 703

Type of genus: *Oestrimyza fenestrata*, new species.

Large flies which are related to *Oestranthrax* Bezzi. The proboscis is reduced to a minute bilateral spur that protrudes downward from a small, sunken, oval recess.

The wing is large and entirely dark yellow brown, with 9 small, yellow, barlike and windowlike spots. The wing is so large that the fly suggests *Poecilanthrax* Osten Sacken in a superficial way and like it the wings are much longer than the abdomen. There are only 2 submarginal cells; the first posterior cell is scarcely narrowed; the anal cell is open although narrowly.

These flies are found in Brazil.

Length: 14 mm.; wing 15 mm.

Head, lateral aspect: Hemiglobular, the occiput prominent, although strongly sloping inward, and the occipital pile scanty, appressed, flat, and rather wiry. There is a small outward swelling of the occiput, at the deepest point of the long, comparatively deep indentation. Eye facets not bisected. The upper occiput is twice as long as the lower occiput. Central fringe rather long and loose and longer above. The front is a little swollen, distinctly visible above the eyeline and more prominent below. Its pile is quite bristly, short, erect, or curled forward. The lower part of the front protrudes almost the length of the two short first antennal segments. The face is strongly swollen forward, convex and rounded, and abruptly rounded below at the lower fifth of the head where there are deep, ventrally widening fissures, rather triangular in form, which constitute the tentorial fissure and pit. The pile of the face is dense and quite bristly, a little longer below, and with the more or less narrow, bare encircling band or line, curving up to the base of each antenna. Proboscis is reduced to a minute, bilateral spur protruding downward from a small, sunken, oval recess; at the posterior end of the spur is a pair of small, seedlike, adjacent, bulbous structures, which may be part of the proboscis or part of the palpus. The antennae are attached slightly above the middle of the head.

Head, anterior aspect: Eyes of the male are rather widely separated by 3 times the width of the low yet abrupt ocellar tubercle. Ocellar triangle short isosceles, and placed far forward from the posterior eye corners, which are unusually broadly rounded, and almost obliquely truncate. The antennae are widely separated by nearly the length of the long third segment and distant from the eye margin by the length of the first two segments. There is an impressed line down the middle of the face. Viewed from above the occipital lobes have a deep, vertical gap or fissure between them, and therefore they are not in contact.

The antennae though conspicuous are not exceptionally large. The first segment is short, a little widened medially, and a little shorter than its apical width. It bears a hemicirclet of short, stiff, bristly setae, but none below. Second segment quite short, small, beadlike, the edges rounded, attached narrowly to the third segment. The third segment has a rounded, short, bulblike base, very gradually tapering above and below into the long, quite thick, bristle-tipped style. Viewed from above the style, which is dorsoventrally flattened, is more than half as wide as the base. Viewed laterally it is less than half as wide, and the apex is bluntly truncate and con-

tains the stubby, asymmetrically placed spine. Head strongly subquadrate from the anterior view.

Thorax: A little longer than wide, the scutellum excepted. A little widened across the prominent postalar callosities, which are not set off by more than the most shallow crease. Color black, surface greasy. The humerus and postalar callosities are brown, the scutellum likewise. Pile of mesonotum fine, short, partly erect, and partly curled downward. The anterior collar is quite short and narrow, but includes the humerus. There are 3 short bristles on the notopleuron, and a patch of short bristly pile between the notopleuron and the humerus and a similar patch on the upper mesopleuron, which is somewhat convexly swollen outward, leaving a flat, narrow, wedge-shaped depression between it and the slightly convex, pilose pteropleuron. Metapleuron with pile. Hypopleuron bare. There appears to be a minute hair tuft under the haltere. Squamal scales short.

Legs: Rather poorly developed and comparatively slender, the anterior pair only a little reduced. All of the legs are rather spiky with short, oblique, numerous, black, spiculate bristles. There are fine bristly setae on the anterior femur. Anterior tibia with 15 or more distinct dorsal bristles, nearly as many anteriorly and posteriorly. The short bristles in the middle femur with 8 or 10 bristles anteroventrally. Hind femur also with 8 or 10 bristles, mostly on the outer half, some of them finer, and all of them less stout than the short bristles of the tibia. Middle and hind tibiae with numerous, conspicuous, stout, short bristles. On the hind tibia there are 3 or 4 rows dorsally and extending somewhat downward laterally, and with 2 ventral rows. Only those of the dorsomedial row are shorter and finer. The more lateral of the dorsal rows contains 20 or more bristles. All tarsi are strongly setate below. Claws fine, slender, sharp, only slightly curved, with no basal tooth, and pulvilli rudimentary or wanting.

Wings: The wings are very large and broad, pointed only at the immediate apex. Like *Poecilanthrax* Osten Sacken they are much longer than the abdomen. The entire wing is dark yellowish brown, rather flat or scarcely wrinkled. The wing has 9, small, yellow, windowlike spots, a bar on each side at the lower end of the second basal cell, again on each side at the upper end of the second basal cell, on each side of the anterior intercalary vein which are extended proximally on the distal portion of the medial crossvein and again on each side of the basal, plane part of the medial crossvein; also spots on both sides of the anterior crossvein and the base of the second vein, on both sides of the base of the anterior branch of the third vein and again on the outer bend of this vein. There is a trace of this yellow color at the base of the second basal cell. There are only 2 submarginal cells, the first posterior cell is scarcely narrowed. The anterior crossvein enters the discal cell at the middle, and the second vein arises a little before the anterior crossvein. Anal cell open, but narrowly. The ambient vein is complete. The alula is about 3 times as long as wide. The basal comb is of moderate width,

with numerous short, oblique setae, and the costal hook is stout basally, sharp at apex.

Abdomen: The abdomen is rather elongate, nearly twice as long as the mesonotum, the scutellum excepted. It is distinctly wider than the thorax and has parallel sides to the end of the sixth tergite. Third to sixth tergite of nearly equal length. The abdomen is greasy, blackish, with the lateral margin of the tergites extending over, with rounded edges, but not curled over. The tergites laterally are dark reddish brown. The pile of the abdomen is minute, flat-appressed and setate, and very little longer along the lateral margins of the tergites. First tergite with slightly longer pile, but confined to the outer edges only. Seven tergites are visible from above, the seventh is nearly or quite as long as the sixth, but rounded laterally. The male terminalia extend downward as an asymmetrically placed cone enclosed by the last sternite.

Material available for study: The unique male type found among flies studied from miscellaneous collections in the National Museum of Natural History.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Neotropical: *Oestrimyza fenestrata*, new species.

Genus *Marleyimyza* Hesse

FIGURE 174

Marleyimyza Hesse, Ann. South African Mus., part 3, vol. 35, p. 521, 1956b. Type of genus: *Marleyimyza natalensis* Hesse, 1956, by original designation; one species.

Large, obese flies, related to *Oestranthrax* Bezzi, larger in size, with shorter, stouter legs and much longer hairs on the femora. Basal tarsal segment more thickened and claws without basal tooth. Separation of male eyes much less than in *Oestranthrax* Bezzi; the genae are very much narrower, according to Hesse (1956). The buccal cavity is broadly visible and not slitlike. The proboscis is more distinct, about equal in length to the third antennal segment. The head is much larger and broader, the indentation of hind eye margin scarcely noticeable. Third antennal segment larger at base and the stylete portion thicker. Hesse says that the buccal cavity is a little less reduced than in *Oestranthrax* Bezzi but much better developed than in *Villostrus* Paramonov.

A unique character of the only known species is the presence of dense, golden yellow hairs on the posterior sternites, which Hesse (1956) notes is somewhat similar to, perhaps a mimic of, the scopae of a gastrilegous bee such as *Megachile*.

All of these several genera, including *Oestrimyza* Hull, are closely related and form a distinct subgroup of the Exoprosopinae.

Marleyimyza Hesse is known from a single male from Natal. Type in South African Museum.

Length: 17 mm.; of wing 15.5 mm.

As I have not been able to see or obtain material of *Marleyimyia* Hesse, I quote Hesse's description of the genus:

From both *Oestranthrax* Bezzi and *Villoestrus* Paramonov this new genus differs in the following respects:

Body larger, mesopleuron distinctly much more convexly bulging and prominent. Head relative to body much larger, more like that of *Villoestrus* Paramonov being quite broad across disc of thorax at level of wings; eyes as in *Villoestrus* Paramonov more than twice as high as long at level of indentation; facets much coarser, those in upper part in male distinctly coarser than in lower part and coarser than in *Villoestrus* Paramonov; interocular space on vertex in male much narrower than in *Oestranthrax* Bezzi, but like that of *Villoestrus* Paramonov: face slightly less convex and also less so than in latter genus; buccal cavity slightly less reduced than in most species of *Oestranthrax* Bezzi, but distinctly much more developed than in *Villoestrus* Paramonov and in form of a broad and deepish depression bounded on each side by somewhat prominent rims or lips; genae very much narrower than in *Oestranthrax* Bezzi and also narrower than in *Villoestrus* Paramonov; rudimentary proboscis like that of former, its labellar part however pointed, not ending in two vestigial lobes; palps also very similar; antennae more like those of latter genus and joint 3 much more broadened at base than in *Oestranthrax* Bezzi, its slender part also relatively shorter than in latter and not so long and filiform. Vestiture with the hairs and scales on first antennal joints and face distinctly longer and very much and markedly denser than in both the other two genera; hair on thorax above discally and anterolaterally, on pleurae, coxae, in metapleural tuft, on scutellum, first tergite, basal half of tergite 2 and base of venter distinctly very much longer, denser, more shaggy in appearance than in former two genera; hairs on sides of abdomen also distinctly longer and denser; those on venter markedly dense, much denser and longer than in any other Exoprosopine and having a marked resemblance to the scopae of a gastrigeous bee; scales on face narrowish as in *Villoestrus* Paramonov, but very much longer; that in form of whitish transverse bands across bases of tergites in narrower bands than in *Oestranthrax* Bezzi, more like those of *Villoestrus* Paramonov, but with a more conspicuous band across base of tergite 3, but none across base of 2 as in former genus; rest of scaling on abdomen above dark or blackish, without any yellowish or ochreous ones.

Legs: Shorter and stouter than in *Oestranthrax* Bezzi, more like those of *Villoestrus* Paramonov, but with much longer hairs on femora; femora, tibiae, and tarsi more or less equal in length as in latter genus; femora without any spines or spinelets below; front tibiae with more and denser spicules than in *Oestranthrax* Bezzi; basal joint of tarsi more thickened than in latter genus; claws without a basal tooth, slightly stouter and more bent down apically than in former two genera. Hypopygium of male very similar to that of *Oestranthrax* Bezzi and those of the *teuochila*-section of *Villa*, but aedeagus much shorter, the scoop-like aedeagal process more rounded knob-like apically and the basal strut more slender.

Wings: More like those of *Villoestrus* Paramonov, with similar venational characters, but not infuscated along costal part or with a dark cross band; second vein slightly less recurved apically than in *Oestranthrax* Bezzi; second submarginal cell longer and narrower basally; second and third posterior cells much shorter, the latter extending basally to much nearer apex of second basal cell; fourth posterior cell tending to be very broad apically, broader than in the other two genera; anal cell closed apically and with a very short stalk in this unique male at least; basal hook of wings longer, more developed than in either genus, more prong-like; squamae with the apical demarcated part considerably shorter than in *Villoestrus* Paramonov.

Since I have not been able to see males of this genus I quote the remarks of Dr. A. J. Hesse with respect to genitalia:

Hypopygium of male very similar to that of *Oestranthrax* and those of the *teuochila*-section of *Villa*, but aedeagus much shorter, the scoop-like aedeagal process more rounded knob-like apically and the basal strut more slender.

Material available for study: None.

Immature stages: Unknown largely. However, the collector of the single male type stated that the fly emerged from an old log containing cossid larvae (Hesse, 1956).

Ecology and behavior of adults: Not recorded.

Distribution: Ethiopian: *Marleyimyia natalensis* Hesse, 1956.

Genus *Exoprosopa* Macquart

FIGURES 197, 198, 208, 210, 376, 680, 747, 971, 972

Exoprosopa Macquart, *Dipteres exotiques*, vol. 2, pt. 1, p. 35, 1840. Type of genus: *Bibia capucina* Fabricius, 1781, as *Anthrax pandora* Macquart, 1826. Designated by Coquillett, p. 544, 1910, the ninth of 41 species.

Mima Megerle in literature, in Meigen, 1820, p. 175.

Trinaria Mulsant, *Mem. Acad. Sci. Lyon*, ser. 2, vol. 2, p. 20, 1852. Type of subgenus: *Anthrax rutila* Pallas in Wiedemann, 1818, as *Anthrax interrupta* Mulsant, 1852. Designated by Coquillett, p. 617, 1910, the first of 2 species.

Argyropsylla Rondani, *Dipterologiae Italicae Prodrum*, vol. 1, p. 162, 1856. Type of subgenus: *Anthrax jaccus* Fabricius, 1805 (*jaccus*), by original designation; one species.

Defitippia Lioy, *Atti. Instit. Veneto*, ser. 3, vol. 9, p. 733, 1864. Type of subgenus: *Anthrax minos* Meigen, 1804. Designated by Griffini, p. 42, 1896.

Argyropsilla Verrall in Scudder, *Nomenclator Zoologicus*, U.S. Nat. Mus. Bull. 19, part 1, p. 32, 1882; emendation.

Eroptata Coquillett, *Canadian Ent.*, vol. 19, p. 13, 1887a; as a genus, now regarded as a subgenus. Type of subgenus: *Exoprosopa divisa* Coquillett, 1887, by monotypy.

Mesoclis Bezzi, *The Bombyliidae of the Ethiopian Region*, p. 229, 1924. Type of subgenus: *Anthrax pygmalion* Fabricius, 1805, by original designation.

Metapenta Bezzi, *The Bombyliidae of the Ethiopian Region*, p. 230, 1924. Type of subgenus: *Exoprosopa pentata* Macquart, 1840, by original designation.

Acrodisca Bezzi, *The Bombyliidae of the Ethiopian Region*, p. 234, 1924. Type of subgenus: *Exoprosopa angulata* Loew, 1860, by original designation.

Cladodisca Bezzi, *The Bombyliidae of the Ethiopian Region*, p. 243, 1924. Type of subgenus: *Exoprosopa suffusa* Klug, 1832, by original designation.

Pterobates Bezzi, *The Bombyliidae of the Ethiopian Region*, p. 273, 1924. Type of subgenus: *Anthrax apicalis* Wiedemann, 1821, by original designation.

Zygodiola Bezzi, *Bull. Soc. Roy. Ent. d'Egypte*, vol. 9, p. 268, 1926c. Type of subgenus: *Anthrax algira* Fabricius, 1794, by original designation.

Corycetta, new subgenus. Type of subgenus: *Exoprosopa subfasciata* Engel, 1936.

Osten Sacken (1886), p. 87, key to 3 species.

Coquillett (1892b), p. 123, key to 9 species from western United States.

Williston (1901), pp. 269-270, key to 11 species from Mexico.

White in Hardy (1924), p. 74, key to 4 Australian species.

Bezzi (1924), pp. 231-236, key to 18 species; p. 246, key to 3 species; pp. 250-252, key to 21 species; p. 274, key to 3 species; pp. 277-286, key to 105 species.

Séguy (1926), pp. 184-185, key to 15 species from France.

Paramonov (1928), pp. 181-303, 6 pl., key to Palaearctic species.

Curran (1930), pp. 2-4, key to 37 species from Mexico and the United States.

Maughan (1935), pp. 34-38, key to 12 species from Utah.

Engel (1936), pp. 454-464, key to 67 Palaearctic species.

Austen (1937), pp. 162-164, key to 14 species from Palestine.

Hesse (1956b), pp. 658-726, key to 171 males and 187 females of species and subspecies.

Johnson and Johnson (1958), pp. 84-85, key to 28 species from western United States.

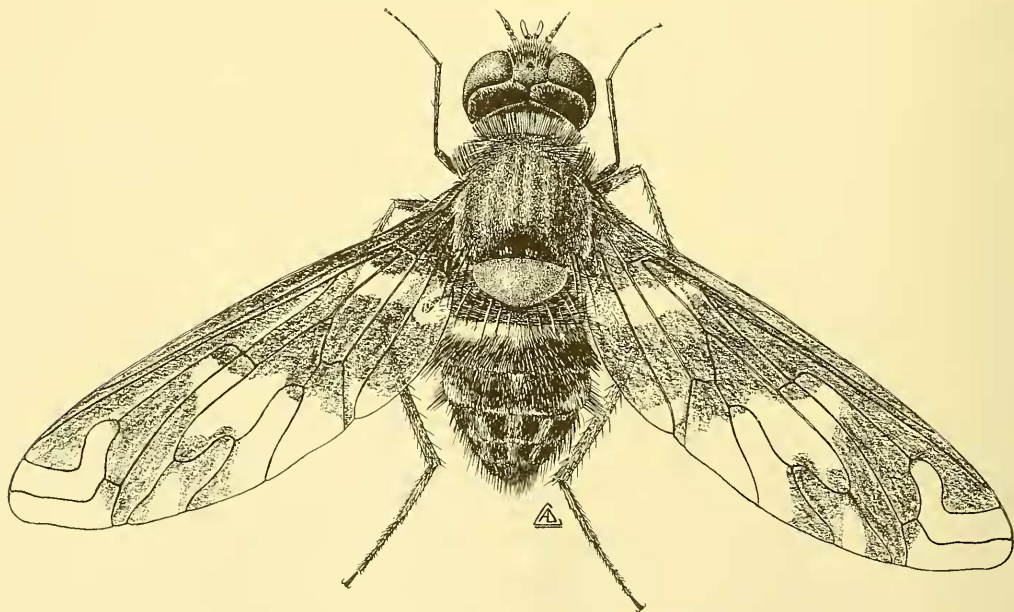
Bowden (1964), pp. 118-119, key to 15 species from Ghana.

Painter and Painter (1969), pp. 5-33, key to species of north neotropical sector.

This is a genus of large flies; occasionally depauperate individuals as little as 6 mm. in body length and 14 mm. in wing expanse, but most species are much larger and some of these species comprise the largest known bee flies. The head is large, subglobular, and loosely attached to the thorax; the occiput is extensive but slopes strongly backward to the margin of the large, deep, central recess. The face is either bluntly protuberant, or very frequently acutely conical. The antennae are relatively small, very widely separated. The third segment is characteristically attenuate and has an articulate, separated, apical, bristle-tipped style; this character with rare exceptions separates *Exoprosopa* Macquart and allied genera from the *Villa* Lioy group of

related genera. The antennal style is without an apical whorl of hairs such as found in the Anthracinae. The proboscis in *Exoprosopa* Macquart is slender, varying from no longer than the oral recess to others where it is almost twice as long.

The flies of this genus can usually be selected out of any assortment of bee flies by the combination of the globular head, conical or subconical face, small, slender, relatively short, widely separated antennae, broadly oval, moderately convex abdomen, together with the large wings, which within the genus show a variety of patterns. The three principal types are species in which: (1) the whole wing is diffusely brown, paler posteriorly; (2) the anterior foreborder is rather sharply brown, the vein closing the second basal cell infuscated; and (3) the wing shows 2 major, generally sharply defined, irregular crossbands, the first one occupying the basal half of the wing and itself sometimes broken into 2 bands, and the second major band proceeding chiefly backward from the apex of the costal cell. This basic pattern of markings assumes many variations, often filling out the whole of the auxiliary cell, often having clear sinuses about the crossveins; the color of this maculation varies from very dark sepia to brownish yellow or combinations of these colors. Presumably all species with completely hyaline wings such as *chionea* Bezzi, *ancilla* Bezzi, *chrystallina* Bezzi, and others should be assigned to *Micomitra* Bowden.



TEXT-FIGURE 46.—Habitus, *Exoprosopa rhea* Osten Sacken.

- 10 (11). Front tibiae short and thick, beset with well-developed spicules; first posterior cell always open iv. *Aceradisca*, subgen. nov.
- 11 (10). Front tibiae long and thin, smooth; first posterior cell often closed and stalked v. *Cladodisca*, subgen. nov.
- 12 (5). Discoidal cell without apical projecting angle below, and if sometimes dilated, dilatation rounded, not angular, and at any rate devoid of appendix.
- 13 (16). Vein between discoidal and second posterior cells long, deeply and regularly S-shaped, and in same line with longitudinal axis of wing, or nearly so; wings never dimidiate; discoidal cell narrow and long, not expanded above or below before distal extremity.
- 14 (15). First posterior cell closed, terminating bluntly, and provided with a long stalk; hind tibiae with very short spicules; wings with the basal half yellow and margined with brown vii. *Triaria* Mulsant.
- 15 (14). First posterior cell usually open, or, if closed, terminating in a narrow apex and with a short stalk; hind tibiae with long and stout spicules; basal half of wings not yellow nor margined with brown viii. *Defilippia* Lány.
- 16 (13). Vein between discoidal and second posterior cells short, straight or only faintly sinuous (if deeply sinuous, then short, or not regularly S-shaped, or forming an angle with longitudinal axis of wing); wings sometimes expanded above or below before distal extremity.
- 17 (18). Legs feathered; discoidal cell contracted in middle; upper branch of cubital fork not widely divergent from main stem; marginal cell very narrow at end ix. *Pterobates*, subgen. nov.
- 18 (17). Legs not feathered.
- 19 (20). Marginal cross-vein straight and not recurrent; second longitudinal vein originating beyond middle cross-vein; first posterior cell typically closed and provided with a short stalk; wings with quite hyaline "window-panes"; abdomen with silvery bands, at least in female x. *Argyrosipita* Rondani.
- 20 (19). Marginal cross-vein sinuous and recurrent; second vein originating opposite or before middle cross-vein; first posterior cell typically open, but sometimes closed; wings never fenestrate, or if so "window-panes" not hyaline; abdomen devoid of silvery bands xi. *Europrosopa* Macquart.

Head, lateral aspect: The head is more or less hemiglobular, its apparent length is increased by the forward extension of the face which ranges from blunt species, like *rostrifera* Jaennicke (compare *Litorrhynchus* Macquart), to those in which the face is conically and acutely produced, like *jacchus* Fabricius. There are large numbers of both the blunt-nosed and conical-nosed species. The occiput dorsally is rather extensive but slopes strongly downward toward the deep, central, cuplike recess. The degree of indentation on the eye varies strongly from species, like *ingens* Cresson, where the excision is so gradual and so slight that the occiput is very little longer opposite the middle of the eye than it is dorsally, to others, like *jacchus* Fabricius, where the indentation is more distinct and angulate with upper and lower angles approximately equal. The pile of the occiput varies from a uniform covering of flat-appressed, scaleiform pile directed outward toward the eye margin, generally touching and overlapping the eye margin, to others in which there is a distinct, pollinose, pile-free rim about the margin of the eye. This

occipital pile gives way medially and centrally to the always short and often scanty interior fringe about the occipital recess. Eyes only slightly reniform. There is a bare triangle at the bottom of the indentation and the line dividing the upper and lower eye facets varies from short to long. Upper eye facets slightly enlarged in the male; some of the lower eye facets tend to be short pilose.

The oragenal opening is long, narrowed in the middle, a little widened anteriorly but much more so posteriorly, with thin, vertical margin posteriorly and the inner wall strongly inflated at the beginning of the tentorial fissure below. The tentorial fissure is linear and deep, leaving only a narrow, sloping margin adjacent to the eye. Cheeks below the eye comparatively prominent. The oragenal recess is quite deep but near the anterior apex sloping up to the facial margin. The head viewed from above shows that the occipital lobes are quite tightly apposed but with a fissure anteriorly and the vertex always shallowly sloped.

The face in *rostrifera* Jaennicke is quite bluntly rounded, extending out about twice the length of the first antennal segment; but in *jacchus* Fabricius the face is more than 3 times as long as the first antennal segment and this segment is about 2 to 3 times as long as its basal width and bears comparatively short, stiff, numerous setae on all sides, except ventrally. The antennal sclerite is distinct but narrow. Second antennal segment disclike, short, from a third to a fourth as long as the first segment and with setae on all sides, except medioventrally. The third segment basally is less wide than the second, somewhat bulbous at the base but with the dorsal surface plane, hence most of the constriction is ventral, to other species that are quite long and conical ending in a more or less attenuate stylar portion, and in all species with an attached segmented style, which varies from one-fourth to one-half as long as the length of the third segment.

Head, anterior aspect: The head is as wide as the thorax, is subquadrate, being rather distinctly flattened on all four sides. The eyes in the male are widely separated by almost as much space as there is between the antennae, seldom as little as two-thirds of the space between the antennae. Females with the eyes not much more separated than in the males. The antennae are very widely separated, the middle space more than twice the distance from the outer edge of the antennae to the eye. The ocellar tubercle is small, quite low, inconspicuous, short isosceles or equilateral, in some species extended backward beyond the ocelli, in others ending abruptly. It is placed well forward beyond the posterior eye corners, which are strongly rounded and the tubercle bears a few short setae in most species. Front sometimes with a sunken depression in the middle on the upper third. Vertex with or without scales.

Thorax: The thorax is comparatively low on the ventral half beneath the wing. It is also rather long. The mesonotum is very little convex, rather flattened posteriorly, pollinose, generally blackish, but some

species have postalar callosity and scutellum pale; the pile varies from dense, fine, flat-appressed hairs, scarcely widened, to others in which the hair is distinctly setate, in still others where they have broad, short scales. In the scalose species there are generally some fine, erect hairs of no great length.

Humerus and the margin as far back as the notopleuron with longer, coarse pile. The anterior collar is very distinct, composed of blunt, dense, long spikelike pile, often of contrasting color. Notopleuron with 3 bristles, often quite stout; postalar callosity with 3 or 4 stout and several more slender bristles; scutellum with 6 to 8 pairs of slender or stout, long bristles. Scutellar disc covered like the mesonotum. The pleuron is thinly pollinose, the mesopleuron densely covered with long, coarse pile, the pile on the upper half sometimes distinctly bristly, and turned upward. Sternopleuron with appressed scales posteriorly and sometimes over nearly the whole surface; they may be very dense. Pteropleuron with bristles and pile and sometimes with scales extensively over the anterior and dorsal part and sometimes with a posteroventral, isolated tuft of setae. The metanotum behind and beneath the scutellum is extremely short, due to the close attachment of the abdomen, laterally there is a tuft of short pile and the swollen metapleuron posteriorly bears a very conspicuous brush of long, coarse pile, sometimes separated into a vertical band posteriorly and an oblique band dorsally. Plumula long, extensive and conspicuous, composed of coarse hairs generally contrasting with the remainder of the pile when the remaining pile is dark. Hypopleuron entirely without pile, except sometimes a few hairs in front of the spiracle.

A conspicuous tuft of flattened scales or hairs is diagonally placed below and behind the spiracle in species like *iota* Osten Sacken, but is completely lacking in other species like *ingens* Cresson. Squama divided by a longitudinal crease with a prominent rim and a fringe of scales that are narrow or sometimes lanceolate and extended onto the alula and base of the axillary lobe. Halteres relatively quite small.

Legs: The femora are stout; the anterior femur slightly thickened basally. Middle and hind tibiae quite stout. The femora are covered with appressed scales varying from jet black to yellowish with besides scattered, suberect, fine setae as a rule, which may become a short, posterior fringe. Middle femur with some stout, spiculate bristles of varying length and thickness and numbers. Hind femur in a species like *ingens* Cresson with as many as 9 or 10 short, quite stout, ventrolateral bristles, in others with 5 or 6, and sometimes with a few quite slender bristles.

The scales on the hind femur and tibia may be so dense and wide as to be quite shinglelike. The anterior tibia bears a dorsal and ventral row of fine, suberect spicules in species like *rostrifera* Jaennicke, in others like *jacehus* Fabricius the anterior tibia is quite slender and bears only very dense, finely appressed microsetae, and, moreover, it is strongly attenuate apically in con-

trast to a group of species like *ingens* Cresson or *rostrifera* Jaennicke where the anterior tibia is actually widened apically. In general all of the tarsi are small, weak, slender, gradually attenuate and short. The anterior tarsi bear a fringe of fine, erect hairs instead of stiff bristles. The anterior claws are minute, the remaining claws large, long, scarcely curved at the apex, sharp apically with a basal tooth and the pulvilli absent.

Wings: Wings large, usually broad at the base, but with exceptions as *ceuthodonta* Hesse, etc., always much longer than the abdomen when at rest. The costal cell ends nearly opposite the base of the first marginal cell. There are 3 submarginal cells, those species having 4 submarginal cells are placed in the very closely related genus *Ligyra* Newman. The pattern of the submarginal group of cells is variable. The kink or bend where these veins are upturned toward the foremargin is either gentle or deep; the veins closing the second submarginal cell and the marginal cell are particularly erratic. From a check of the wings of 90 species, I find that 47 show the second vein arising before the anterior crossvein, and 37 show it precisely arising at the anterior crossvein, while 6 species show it arising beyond this crossvein; in none of the species where it lies before or after the crossvein is it separated from it by more than the length of the crossvein itself, usually less. This second vein usually arises rectangularly, but it is oblique in a few species as *goliath* Bezzi and *argentifrons* Macquart and very gradual in origin in *lacerata* Engel.

In some species the marginal cell is divided into two parts by an extra crossvein and the wing has eyelike spots. This is the basis for the genus *Heteralonia* Rondani. Again the first posterior cell may be divided into two by a supernumerary crossvein, thus leaving 5 posterior cells as in *Exoprosopa divisa* Coquillett. This is the basis for the subgenus *Exoptata* Coquillett, further distinguished by the perfectly smooth, slender, anterior tibia.

Another group of species shows that the discal cell on its lower margin before the apex has a strong, distinct, angular bend, frequently emitting an appendix vein, and the terminal vein of the discal cell sinuous and placed at an angle or perpendicularly or longitudinally to the axis of the wing. Within this group the species having the fourth posterior cell closed and stalked represent the subgenus *Metapenta* Bezzi. Those with the third posterior cell closed and stalked constitute the subgenus *Mesoclis* Bezzi. Each of these have 5 posterior cells. Those with only 4 posterior cells have the first posterior cell always open and the front tibia short and thick and spiculate; these belong to the subgenus *Aerodisca* Bezzi. Those species that have the front tibia long, thin, and smooth and the first posterior cell often closed and stalked belong to the subgenus *Cladodisca* Bezzi. There are several other distinct venational groups; for example, those species that have the vein between the discal and second posterior cells long and deeply and regularly S-shaped, the discoidal cell itself narrow and long constitute another group of subgenera.

I am obliged to agree with Bezzi (1924), who states: "These characters have at least the same value and constancy as the crossvein uniting the 2 branches of the cubital fork in *Hyperalonia* Rondani (*Ligyra* Newman), and may therefore be employed for the purpose of generic or subgeneric division."

In *Exoprosopa* Macquart the anal cell is open, the anal vein is sometimes straight and sometimes strongly sinuous, the alula is moderately extensive and characteristically bears scales similar to those found upon the squama. A few scales are continued basally along the edge of the axillary lobe. The distal end of the alula is always rounded, the ambient vein is complete and in both sexes the costa at base is strongly expanded and flattened, but the comb of spicules which this area bears are minute or coarse. There is a well developed basal hook. The pattern types and coloration of the wing have been dealt with earlier, but it should be noted that the posterior third of the wing is very strongly rippled or fluted transversely.

Abdomen: The abdomen is broadly oval, a little wider than the thorax itself, rather gently convex and in a few species more or less flattened, usually black; it may be sometimes light brownish orange with black medial spots. The pile characteristically consists of dense, slender, linear scales that lie flat-appressed, frequently forming pale bands along the anterior part of one or more and sometimes all of the tergites beyond the first, leaving the posterior margin with black scales. In *jaechus* Fabricius patches on each side of 6 tergites bear dense, flat-appressed, silvery scales making this species look very much like a *Lepidanthrax* Osten Sacken. Sides of the first tergite with the usual bombylid-like brush of dense, erect, coarse pile. Sides of the remaining tergites either with very short, appressed fringes of pile or sometimes with long tufts of erect and suberect, bristly pile, as in *calyptera* Say. There are 7 tergites visible above in the male and female, a very short eighth recessed beneath the seventh. Female terminalia have about 7 pairs of strong spines upon the acanthophorites. The male terminalia are large, elongate, recessed beneath the last tergite but generally visible from below.

Dr. A. J. Hesse was able to study a very large assemblage of species in this genus; for this reason I quote his comments on the male genitalia:

Hypopygium of males very uniform and almost similar in a large number of species, often however strikingly different, suggesting generic differences; the shell-like basal parts invariably hairy on dorsal aspect, sometimes with a few characteristic curved or hook-like, dark, flattened, spine-like setae medially and dorsally between the partly fused basal parts, the apical angle of basal parts sometimes prominently projecting and bases sometimes also produced; beaked apical points always more or less curved, their apical parts directed upwards, their apices usually sharp and in many forms with a slight indentation, giving them a bifid appearance, their outer lateral angles usually prominent, angular, or even bluntly spine-like, and with some hairs, the dorsal surface usually hollowed out or depressed to a variable extent; aedeagus rarely long; a ventral aedeagal process invariably present and well developed, assuming various shapes which are of specific value in the separation

of the species; lateral struts fairly uniform, but sometimes broad or much reduced; basal strut assuming various shapes, much reduced and small in a few species.

The male terminalia from dorsal aspect, epandrium removed, show a figure broad basally, much narrowed on the outer third or less. The epiphallus is rather prominent, narrowing apically, the sides not quite parallel, and the sides nearly plane. In a genus as large as this, the figures must vary greatly. From the lateral aspect the dististyle is quite subapical and incised just before the upturned, hooklike apex. The end of the aedeagus shows a curious cap located vertically over the rather narrow preceding neck; it is notched below. Epandrium large, plane above with a blunt, short, downturned lobe basally.

Hesse finds the hypopygium and terminalia within the male very uniform and almost similar in a large number of species, however, sometimes "strikingly" different, thus suggesting generic differences; the shell-like basal portion he finds invariably with hair dorsally, sometimes with a few curved or hooklike, flattened, spiny setae medially and dorsally between the partly fused basal parts, and with the apical angles of the basal parts sometimes prominently projecting and the base also sometimes produced; he found the dististyli (beaked apical segments) always more or less curved, with their apices directed upward, the apices sharp, often with a slight indentation, which produces a bifid appearance, their outer lateral angles usually prominent, angular or even spinelike. The aedeagus was rarely long, a ventral aedeagal process always present and well developed and assuming various shapes of specific value; the lateral struts were uniform but sometimes broad, or much reduced; basal struts much reduced and small in a few species.

Material studied: Many Nearctic and Neotropical species and some Palaearctic, Ethiopian, and Australian material.

Immature stages: Such stages are known for several species of this genus and such data as we have indicate hyperparasitism on bees, wasps, and beetle larvae that live in the soil. See discussion under life histories.

Ecology and behavior of adults: The adults can be captured either resting upon the ground in sandy places or upon many species of flowers, especially composites, and while arid regions are greatly favored by this genus, about 16 percent of the bee fly fauna of Lafayette County, Mississippi, a temperate region of considerable rainfall, are comprised within the genus *Exoprosopa* Macquart. Certainly many known species have been found in the Mediterranean and in Asia Minor, and the South African fauna is extraordinarily rich in this genus. The wing patterns of over a hundred species have been illustrated by various authors. The flies of this genus have an extraordinarily powerful flight, and the marked strengthening of the costa at its base doubtless has something to do with this and perhaps the fluted wrinkling of the wing as well. Even the most

wary species, however, may be captured by quietly stalking them.

Distribution: Nearctic: *Exoprosopa agassizii* Loew, 1869; *albifrons* Curran, 1930; *anomala* Painter, 1934; *arenicola* Johnson and Johnson, 1959; *bifurca* Loew, 1869; *butleri* Johnson and Johnson, 1959; *californiae* (Walker), 1852 (as *Anthrax*); *caliptera* (Say), 1823 (as *Anthrax*); *celeris* Cole, 1916; *clarki* Curran, 1930; *decora* Loew, 1869; *divisa* (Coquillett), 1887 (as *Exopata*); *dodrans* Osten Sacken, 1877; *dodrina* Curran, 1930; *dorcadion* Osten Sacken, 1877; *doris* Osten Sacken, 1877 [= *pallens* Bigot, 1892]; *eremita* Osten Sacken, 1877 [= *grata* Coquillett, 1892]; *fasciata* Macquart, 1840 [= *americana* (Wulp), 1867 (as *Mulio*), = *longirostris* Macquart, 1850, = *rubiginosa* Macquart, 1840]; *fascipennis* Say, 1824 [= *coniceps* Macquart, 1850, = *melanura* Bigot, 1892, = *philadelphica* Macquart, 1840]; *fascipennis albicollaris* Painter, 1962; *fascipennis noctula* (Wiedemann), 1830 (as *Anthrax*); *fumosa* Cresson, 1919; *hulli* Painter, 1930; *hyalipennis* Cole, 1923; *ingens* Cresson, 1919; *iota* Osten Sacken, 1886; *jonesi* Cresson, 1919; *junta* Curran, 1930; *meigenii* (Wiedemann), 1828 (as *Anthrax*) [= *emarginata* Macquart, 1840]; *painterorum* Johnson and Johnson, 1960 [= *cingulata* Johnson and Johnson, 1959]; *pardus* Osten Sacken, 1886; *pueblensis* Jaennicke, 1867; *rhea* Osten Sacken, 1886; *rostrifera* Jaennicke, 1867; *sharonae* Johnson and Johnson, 1959; *sima* Osten Sacken, 1877; *socia* Osten Sacken, 1886; *sordida* Loew, 1869; *tezana* Curran, 1930; *tiburoniensis* Cole, 1923; *titubans* Osten Sacken, 1877; *utahensis* Johnson and Johnson, 1959; *xanthina* Painter, 1934.

Neotropical: *Exoprosopa anthracoides* Jaennicke, 1867 [= *trabalis* Loew, 1869]; *argentifasciata* Macquart, 1864; *atripes* Cole, 1923; *bipartita* Bigot, 1892; *bizona* Walker, 1850; *blanchardiana* Jaennicke, 1867; *brevirostris* Williston, 1901; *brevistylata* Williston, 1901; *castilla* Painter, 1930; *cubana* Loew, 1869; *extensa* Wulp, 1888; *filia* Osten Sacken, 1886; *flavineris* Macquart, 1846; *fumosa* Cresson, 1919; *harpia* (Wiedemann), 1828 (as *Anthrax*); *interrupta* Wiedemann, 1828; *limbipennis* Macquart, 1846; *maldonadensis* Macquart, 1849; *melanura* Bigot, 1892; *mus* Curran, 1930; *nubifera* Loew, 1869; *orcus* Walker, 1849; *panamensis* Curran, 1930; *parva* Loew, 1869; *pavida* Williston, 1901; *phlegethon* Walker, 1849; *progne* Osten Sacken, 1886; *prometheus* Macquart, 1855; *punctata* Macquart, 1849; *rufiventris* (Blanchard in Gay), 1852 (as *Paranthrax*); *sackeni* Williston, 1901; *santipauli* Macquart, 1840; *sola* Painter, 1939; *spadix* Painter, 1933; *stymphalis* Wiedemann, 1828; *subfascia* Walker, 1849; *uruguayi* Macquart, 1840; *varicolor* Macquart, 1846.

Palaeartic: *Exoprosopa aberrans* (Paramonov), 1928 (as *Zygodiola*); *adelpia* (Becker), 1906 (as *Zygodiola*); *aecus* (Meigen), 1804 (as *Trinaria*) [= *bombyciformis* Dufour, 1833, = *livida* Pallas in Wiedemann, 1818, = *lutea* Macquart, 1840]; *aegina* (Wiedemann), 1828 (as *Trinaria*) [= *bovei* Macquart, 1840, = *bovis* Becker, 1906]; *aegyptiaca* (Paramonov),

1928 (as *Defilippia*); *albicincta* Macquart, 1840; *algira* (Fabricius), 1794 (as *Anthrax*, later as *Zygodiola*) [= *archimedeia* Bigot, 1860, = *pygmalion* Macquart, 1834, not Fabricius, = *sicula* Macquart, 1834, = *singularis* Macquart, 1840]; *ammophila* (Paramonov), 1931 (as *Trinaria*); *antica* Walker, 1871; *anus* (Wiedemann), 1828 (as *Anthrax*); *apicalis* Klug in Loew, 1860; *araxana* Paramonov, 1828; *arenacea* (Becker), 1906 (as *Zygodiola*); *bagdadensis* (Macquart), 1840 (as *Zygodiola*) [= *clausa* Becker, 1913]; *beckeri* Austen, 1913; *bezzi* Paramonov, 1928; *bucharensis* Paramonov, 1929; *busiris* Jaennicke, 1867; *capucina* (Fabricius), 1781 (as *Argyrospyla*) [= *caloptera* Pallas in Wiedemann, 1818, = *dorcadion* Osten Sacken, 1877, = *nigrata* (Wiedemann), 1828 (as *Anthrax*), = *nigrata* (Fabricius), 1775 (as *Bibio*), = *pandora* Macquart, 1826 (not Fabricius)]; *chalybaea* (Roeder), 1887 (as *Pterobates*), *chalybaea chrysogaster* Bezzi, 1926; *chan* Paramonov, 1928; *circoides* (Paramonov), 1928 (as *Defilippia*), *circoides nigrofasciata* Paramonov, 1928; *cleomene* (Egger), 1859 (as *Argyrospyla*); *conspicienda* Austen, 1937; *completa* (Loew), 1873 (as *Zygodiola*); *decrepita* (Wiedemann), 1828 (as *Defilippia*) [= *albifacies* Paramonov, 1928, = *flava* Paramonov, 1928]; *dedecor* (Loew), 1870 (as *Defilippia*), *dedecor minoides* Paramonov, 1928; *dedecoroides* Paramonov, 1928; *deserta* Paramonov, 1928; *dispar* (Loew), 1869 (as *Cladodisca*) [= *rivularis* Griffin, 1892], *dispar interrupta* Paramonov, 1926; *disrupta* Walker, 1871; *dives* Walker, 1849; *dulcis* Austen, 1936; *efflatoun beyi* Paramonov, 1928; *efflatouni* (Bezzi), 1925 (as *Defilippia*); *exoprosopoides* Paramonov, 1928; *fallaciosa* (Loew), 1873 (as *Zygodiola*) [= *evanescens* Becker, 1913]; *ferruginea* Klug, 1832; *fusconotata* Becker, 1913; *grandis* Wiedemann in Meigen, 1820 [= *turcomana* Portschinsky, 1877, = *fasciata* Dufour, 1850]; *griseipennis* Macquart, 1849; *guttipennis* Bezzi, 1924 [= *punctipennis* Ricardo in Forbes, 1903]; *herzi* Portschinsky, 1892; *hyalipennis* Paramonov, 1928; *insularis* (Ricardo in Forbes), 1903 (as *Cladodisca*); *italica* (Wiedemann in Meigen), 1820 (as *Argyrospyla*), *italica megaera* Wiedemann in Meigen, 1820; *jacchus* (Fabricius), 1805 (as *Argyrospyla*) [= *italica* Rossi, 1792, = *jocchus* Fabricius, 1805, lapsus, = *pandora* Meigen, 1820, not Fabricius, = *picta* Wiedemann in Meigen, 1820], *jacchus baccha* Loew, 1869, *jacchus maenas* Loew, 1869, *jacchus quadripunctata* Paramonov, 1928; *kirgizorum* Paramonov, 1928 [= *uzbekorum* Paramonov, 1928]; *lacerata* Engel, 1936; *latiuscula* (Loew), 1873 (as *Zygodiola*) [= *farinosa* Becker, 1913]; *lucidifrons* Becker, 1913; *lugubris* Macquart, 1840; *megerlei* Meigen, 1820 [= *campicola* Eversman, 1854, = *mayeti* Bigot, 1888, = *turanica* Paramonov, 1928, = *vespertilio* Wiedemann in Meigen, 1820], *megerlei consanguinea* Macquart, 1840, *megerlei deserticola* Paramonov, 1928, *megerlei vesperugo* A. Costa, 1893; *melaena* Loew, 1874, *melaena abbreviata* Paramonov, 1928; *melanoptera* Pallas in Wiedemann, 1818; *meridionalis* Paramonov, 1928; *minoana* Paramonov, 1928; *minois* (Loew), 1869 (as *Defilippia*); *minos*

(Meigen), 1804 (as *Anthrax*, later as *Defilippia*) [= *albiventris* Macquart, 1840, = *germari* Wiedemann in Meigen, 1820, = *semialba* Wiedemann, 1818, = *semi-flavida* Becker, 1906, = *senilis* Klug, 1832, = *siderata* Pallas in Wiedemann, 1818], *minos pharonis* Paramonov, 1928; *mucoea* (Klug), 1832 (as *Zygodiola*) [= *bagdadensis* Becker, 1902, not Macquart, syn. of *tephroleuca* Loew, = *tephroleuca* Loew, 1856, = *olivieri* Macquart, 1840, = *sauvipennis* Macquart, 1849]; *munda* Loew, 1869, *munda ricularis* Griffin, 1896; *nigrifera* Walker, 1871; *noctilio* Klug, 1832 [= *marginalis* Walker, 1871]; *nonna* Becker, 1913; *normalis* (Loew), 1869 (as *Zygodiola*); *occlusa* (Loew), 1873 (as *Zygodiola*), *occlusa nubeculosa* Loew, 1870; *occlusoides* (Paramonov), 1928 (as *Zygodiola*), *occlusoides lactea* Paramonov, 1928; *onusta* Walker, 1852 (as *Anthrax*) [= *pectoralis* Loew, 1937, = *truquii* Rondani 1863]; *pallasii* Wiedemann, 1818 [= *dionysii* Bigot, 1860, = *rhyminica* Eversmann, 1854]; *pallidisetigera* Austen, 1937; *pandora* Fabricius, 1805; *pauper* Walker, 1871 (as *Anthrax*); *phacoptera* Meigen, 1820 [= *titanus* Megerle in litt. in Meigen, 1820]; *pictilipennis* Austen, 1936; *pleskei* Paramonov, 1928; *portshinskiji* Paramonov, 1928; *pulcherrima* Paramonov, 1928; *punctinervis* (Becker), 1913 (as *Cladodisca*); *pygmalion* (Fabricius), 1805 (as *Anthrax*, later as *Mesocalis*) [= *delineata* Becker, 1906, = *varinervis* Macquart, 1840, = *zona* Bigot, 1860]; *ricularis* (Meigen), 1820 (as *Cladodisca*) [= *argyrocephala* Macquart, 1840, = *ricularis* Griffin, 1896, = *sabaea* Meigen, not Fabricius, 1804], *ricularis munda* Loew, 1869; *rivulosa* (Becker), 1902 (as *Zygodiola*); *rutila* (Pallas in Wiedemann), 1818 (as *Trinaria*) [= *daubei* Guérin, 1835, = *hilaris* Eversman, 1854, = *interrupta* Mulsant, 1852, = *krugeri* Bezzi, 1926, = *miegii* Dufour, 1850]; *seniculus* Wiedemann, 1828 [= *lugens* Paramonov, 1928]; *serpentata* (Loew), 1854 (as *Argyrospyla*); *shekovenikovi* (Paramonov), 1928 (as *Pterobates*); *similis* Coquillett, 1898, *spiloneura* Bezzi, 1926; *squamea* Mulsant, 1852; *subfasciata* Engel, 1936; *suffusa* (Klug), 1832 (as *Cladodisca*) [= *conturbata* Loew, 1869]; *sytschuana* Paramonov, 1928; *tamerlan* (Portschinsky), 1887 (as *Trinaria*), *tamerlan bezzii* Paramonov, 1928; *telamon* Loew, 1869 [= *loewi* Paramonov, 1928]; *transcaucasica* Paramonov, 1928; *turkestanica* (Paramonov), 1925 (as *Argyrospyla*), *turkestanica mongolica* Paramonov, 1928; *uzbekorum* Paramonov, 1928, female of *uzbekorum* = syn. of *kirgizorum* Paramonov, 1928; *vassiljevi* Paramonov, 1928; *vlavovi* Paramonov, 1928; *volitans* Wiedemann, 1828; *zimini* Paramonov, 1929; *zanoni* (Bezzi), 1922 (as *Argyrospyla*); *zurudnyi* Paramonov, 1928.

Ethiopian: *Eroprosopa acrodiscoides* Bezzi, 1921; *acrosphila* Bezzi, 1923; *albata* Bezzi, 1924, *albata novaeformis* Bezzi, 1924; *albofimbriata* Bezzi, 1924; *albonigra* Bezzi, 1924; *altaica* Paramonov, 1925; *angulata* Loew, 1860; *angusta* Bezzi, 1924; *aphelesticta* Hesse, 1956; *apicalis* Wiedemann, 1821; *apiformis* Hesse, 1956; *arcuata* Macquart, 1847; *argentifrons* Macquart, 1855, *argentifrons scalaris* Bezzi, 1924; *argillocosmia* Hesse,

1956; *argyrophora* Bezzi, 1912; *aridicola* Hesse, 1956; *atrata* Hesse, 1956; *atrella* Hesse, 1956; *atrinasis* Speiser, 1910; *atrisquama* Hesse, 1956; *aululans* Bezzi, 1924; *balioptera* Loew, 1860; *barnardi* Hesse, 1956; *basalis* Ricardo, 1901; *basifascia* Walker, 1849 (as *Anthrax*); *batrachoides* Bezzi, 1912; *bolhocera* Hesse, 1956; *brachipleuralis* Hesse, 1956; *brevinasis* Bezzi, 1924; *cadericina* Bezzi, 1924; *cafra* Wiedemann, 1821; *caffrariana* Hesse, 1956; *campestris* Hesse, 1956; *capensis* Wiedemann, 1921; *capnoptera* Bezzi, 1912; *cervina* Bezzi, 1921; *ceuthodonta* Hesse, 1936; *cingularis* Hesse, 1956; *claripennis* Hesse, 1956; *clathrata* Bezzi, 1923; *clausina* Bezzi, 1924; *compa* Bezzi, 1924; *connivens* Bezzi, 1924; *conochila* Bezzi, 1924; *contorta* Bezzi, 1924; *corvina* Loew, 1860; *corvinoides* Hesse, 1956; *costalis* Macquart, 1846; *curvicornis* Bezzi, 1924; *damarensis* Hesse, 1956; *decastroi* Hesse, 1950; *decipiens* Bezzi, 1924; *decolor* Bezzi, 1924; *didesma* Hesse, 1956; *dilatata* Bezzi, 1921; *diluta* Bezzi, 1924; *dimidiata* Macquart, 1846; *discriminata* Bezzi, 1912; *dolichoptera* Bezzi, 1924; *dubia* Ricardo, 1901; *dux* Wiedemann, 1828; *elipsis* Bezzi, 1924; *elongata* Ricardo, 1901; *chuta* Loew, 1860; *engyoptera* Hesse, 1956; *erebus* Walker, 1849 (as *Anthrax*); *evemochara* Hesse, 1956; *exigua* Macquart, 1855 [= *tenuis* Macquart, 1855]; *fastidiosa* Bezzi, 1924; *ferreirae* Hesse, 1950; *fimbriatella* Bezzi, 1921, *fimbriatella furvalis* Hesse, 1956; *flavicans* Bezzi, 1924; *formosula* Bezzi, 1921; *fulviops* Szilady, 1942; *furvipennis* Hesse, 1956; *fuscula* Bezzi, 1924; *gentilis* Bezzi, 1924; *goliath* Bezzi, 1924; *gonioneura* Hesse, 1956 [= *spoliata* Bezzi, 1922]; *grigua* Hesse, 1956; *guillarmodi* Hesse, 1956; *hamata* Macquart, 1840; *hamula* Hesse, 1956; *haustellata* Bezzi, 1924; *hemiphaea* Hesse, 1956; *heterocera* Bezzi, 1912; *heros* Wiedemann, 1819, *heros litoralis* Hesse, 1956, *heros melanthia* Hesse, 1956, *heros protuberans* Bezzi, 1924; *hyalodisca* Bezzi, 1923; *hyaloptera* Hesse, 1956; *hypargira* Bezzi, 1921; *hypargyroides* Hesse, 1956; *hypomelaena* Bezzi, 1912; *ignava* Loew, 1860; *inaequilipes* Loew, 1852 [= *peociloptera* Bezzi, 1924, = *hirtipes* Loew, 1860]; *indecisa* Walker, 1849 (as *Anthrax*); *infumata* Bezzi, 1924; *infumata* Bezzi, 1921; *inornata* Loew, 1860; *jacchoides* Bezzi, 1912; *jubatipes* Hesse, 1956; *kaokoensis* (Hesse), 1956 (as *Heteralonis*); *karooana* Hesse, 1956; *laeta* Loew, 1860; *latifrons* Bezzi, 1924; *lepidogastra* Bezzi, 1912; *leucothyrida* Hesse, 1956; *linearis* Bezzi, 1924; *loewiana* Bezzi, 1924; *loxosphila* Hesse, 1956; *luctifera* Bezzi, 1912; *luteicincta* Hesse, 1956; *luteicosta* Bezzi, 1921, *luteicosta metapleuralis* Hesse, 1956; *luteocera* Hesse, 1956; *macroptera* Loew, 1860 [= *longipennis* Loew, 1863, sine descr.]; *maculifer* Bezzi, 1921; *maculosa* Wiedemann, 1819; *madagascariensis* Macquart, 1849; *magnipennis* Bezzi, 1924; *major* Ricardo, 1901; *majuscula* Hesse, 1956; *maria* Walker, 1849 (as *Anthrax*); *marleyi* Hesse, 1956; *masienensis* Hesse, 1950; *melanaspis* Bezzi, 1924; *melanostola* Hesse, 1956; *melanozona* Hesse, 1956; *merope* Wiedemann, 1824; *mesopleuralis* Bezzi, 1924; *metopargyra* Hesse, 1956; *mimetica* Hesse, 1956; *mira* Hesse,

1936; *monticola* Hesse, 1956; *morosa* Loew, 1860; *mozambica* Hesse, 1956; *mydasiformis* Bezzi, 1924; *nebulosa* Hesse, 1956; *nigerrima* Bezzi, 1924; *nigrovenosa* Bezzi, 1924; *nemesis* Fabricius, 1805 [= *nox* Walker, 1849]; *nephoneura* Hesse, 1950; *neurospila* Bezzi, 1921; *nigrifimbriata* Hesse, 1956; *nigrina* Bezzi, 1924; *nigripennis* Loew, 1852; *nigrispina* Bezzi, 1924; *nigritella* Bezzi, 1924; *notabilis* Macquart, 1840 [= *teufiki* Paramonov, 1931]; *nova* Ricardo, 1901; *nuragasa* Hesse, 1956; *obscurinotata* Hesse, 1956; *obscuripennis* Hesse, 1956; *obtusa* Bezzi, 1924; *offuscata* Bezzi, 1921; *ogilviei* Hesse, 1956; *othello* Szilady, 1942; *ovamboana* Hesse, 1956; *pallida* Bezzi, 1924; *pallidifacies* Hesse, 1956; *pallidipes* Hesse, 1956; *palustris* Bezzi, 1924; *parvula* Bezzi, 1921; *paucispina* Hesse, 1956; *pentalia* Macquart, 1840; *penthoptera* Bezzi, 1956; *personata* Bezzi, 1921; *perpulchra* Bezzi, 1924; *plerosticta* Hesse, 1956; *pleroxantha* Hesse, 1936; *polyspila* Bezzi, 1924; *polysticta* Hesse, 1956; *porcicella* Hesse, 1956; *poricella* Hesse, 1956; *praefica* Loew, 1860; *pterosticta* Hesse, 1936; *punctifrons* Bezzi, 1924; *punctulata* Macquart, 1840; *pusilla* Macquart, 1840 [= *jaechoides* Bezzi, 1924]; *rasa* Loew, 1860; *rectifascia* Bezzi, 1924; *recurrens* Loew, 1860; *referta* Bezzi, 1924; *reticulata* Loew, 1860; *retracta* Bezzi, 1924; *rhodesiensis* Hesse, 1956; *robertii* Macquart, 1840; *rubella* Bezzi, 1924; *rubescens* Bezzi, 1924; *rubicunda* Hesse, 1956; *rutiloides* Bezzi, 1924; *sabulina* Becker, 1913; *saskae* Szilady, 1942; *scaligera* Bezzi, 1912; *schmidtii* Karsch, 1887; *senegalensis* Macquart, 1840; *sigmoidea* Bezzi, 1912; *simillima* Hesse, 1956; *sisypus* Fabricius, 1805; *spectrum* Speiser, 1910; *spoliata* Bezzi, 1924; *stannusi* Bezzi, 1912; *stenometatena* Bezzi, 1924; *stevensoni* Hesse, 1956; *strenua* Loew, 1860; *suffusipennis* Bezzi, 1923; *tabanoides* Bezzi, 1924; *thoracica* Bezzi, 1924; *tollini* Loew, 1863; *tricolor* Macquart, 1840; *tricolor orientalis* Bezzi, 1924; *trigradata* Hesse, 1956; *triloculina* Hesse, 1956; *tripartita* Hesse, 1956; *triplex* Bezzi, 1924; *tuckeri* Bezzi, 1921; *umbrosa* Loew, 1860; *unifasciata* Ricardo, 1901; *venosa* Wiedemann, 1819; *villaeformis* Bezzi, 1912; *villosa* Bezzi, 1924; *violaceo* Bezzi, 1924; *vum-buensis* Hesse, 1956; *zambesiana* Hesse, 1956; *zonata* Hesse, 1936; *parva* Ricardo.

Oriental: *Exoprosopa abjecta* Nurse, 1922; *abrogata* Nurse, 1922; *affinissima* Senior-White 1924; *albida* Walker, 1852; *alexon* Walker, 1849; *annandalei* Brunetti, 1909; *aurantiaca* Guerin, 1835; *auriplena* Walker, 1852; *bengalensis* Macquart, 1840; *binotata* Macquart, 1855; *brahma* Schiner, 1868; [= *bramah* Wulp, 1896, lapsus]; *collaris* Wiedemann, 1828 [= *ruficollis* Saunders, 1841]; *dissoluta* Nurse, 1922; *flammea* Brunetti, 1909; *flavipennis* Brunetti, 1909; *flaviventris* Dolschall, 1857; *fuscipennis* Macquart, 1848; *gujaratica* Nurse, 1922; *insulata* Walker, 1852; *interstitialis* Nurse, 1922; *iridipennis* Nurse, 1922; *javana* Macquart, 1840; *lateralis* Brunetti, 1909; *latipennis* Brunetti, 1909; *maculiventris* Brunetti, 1920; *niveiventris* Brunetti, 1909; *obliqua* Macquart, 1840; *pennata* Nurse, 1922; *pennipes* Wiedemann, 1821; *puerula* Brunetti, 1920; *punjabensis*

Nurse, 1922; *purpuraria* Walker, 1852; *retrorsa* Brunetti, 1909; *semilucida* Walker, 1852; *sipho* Paramonov, 1928; *siva* Nurse, 1922; *stylata* Brunetti, 1920; *tristis* Wulp, 1868; *umbrifer* Walker, 1849; *vitrea* Bigot, 1892; *vitripennis* Brunetti, 1912.

Australian: *Exoprosopa adelaidica* Macquart, 1855; *bicellata* Macquart, 1847; *dimidiata* Roberts, 1928; *latelimbata* Bigot, 1892; *obliquefasciata* Macquart, 1849; *stellifer* Walker, 1849.

Oceania: *Exoprosopa alternans* Macquart, 1855; *sinuatifascia* Macquart, 1855.

Country Unknown: *Exoprosopa argentifera* Walker, 1849; *marginicollis* Gray in Griffiths, 1833; *pulehra* Walker, 1852; *thomae* Fabricius, 1805; *umbra* Walker, 1849; *undans* Walker, 1849.

Genus *Atrichochira* Hesse

FIGURES 206, 431A, 711, 721

Atrichochira Hesse, Ann. South African Mus., vol. 35, p. 911, 1956. Type of genus: *Exoprosopa pediformis* Bezzi, 1921, by original designation.

A rather curious, yellowish to reddish-brown fly of medium size with black mesonotum and related to *Exoprosopa* Macquart. The stylate part of the third antennal segment is thickish, and the division into the apical segment of the style is not easily found; this microsegment is apically pointed, and about 5 times as long as wide; there is a spinous bristle at the end of the style. The face is more rounded and tumid than *Exoprosopa* Macquart, and the mesonotum and scutellum have the bristles very weak or absent; unlike *Exoprosopa* Macquart the head is entirely light red, the proboscis quite short. Hesse (1956) notes further that the legs have the spines very weak and reduced and the basal tooth of the claw minute, short and spinelike. The anterior tarsi are appressed setate instead of hairy. There is a sharp and characteristic bend in the vein on the lower side of the discal cell, this vein arises rectangularly from the last branch of the fifth vein, makes a sharp bend outward, and emits a backward spur at the angle. Hesse notes that the dististyli of the male genitalia differ from most *Exoprosopa* Macquart by being hook-shaped, the beak curved upward and outward, not bifid or notched.

Two species have been placed here. One, the type-species, occurs in the southern part of the Cape Province, Zululand, and Natal, and a second species, *inermis* Bezzi, is from Nyasaland.

Length: 10 to 13 mm.; wing a trifle shorter.

Head, lateral aspect: Subglobular, the occiput is comparatively prominent although strongly rounded backward and inward. The occipital cup is deep but relatively small; occipital pile scanty, flat-appressed, and a little flattened. The front is long and convex and moderately protuberant especially on the lower half, its pile scanty, rather short, stiff, and erect. The face is

quite prominent, bluntly or obtusely conical, its length above the oral recess is at least as long as the small antenna; facial pile also scattered and scanty, bristly and suberect. The eye is large, the upper facets in the male scarcely enlarged, and the indentation in the middle of the posterior eye margin, although quite broad, is quite shallow also. There is a bisecting line in the middle of the eye posteriorly. The proboscis is quite short but also slender, the slender labellum comprises more than the outer third and the slender, long palpus reaches almost to the labellum and has a fine, apical, and lateral fringe of short hairs. The proboscis is enclosed in the narrow oral recess and does not reach to the apex of the face. The antennae are attached a little above the middle of the head in profile. They are small and the first segment is nearly twice as long as the second; the second segment is about half as long as wide; the third segment forms a triangular cone at the base, broadly attached to the second segment and not wider than this segment. Apically the third segment is drawn out into a narrow style with bristle at tip and no additional microsegments; the style is not quite as long as the remaining antenna. The first antennal segment bears only a few short setae.

Head, anterior aspect: Head not quite as wide as the thorax, almost circular and at most slightly flattened laterally and at the vertex. The vertex is level with the eye margin; the minute ocellar triangle is very low, equilateral or obtuse, and is set a considerable distance forward from the posterior eye corners. The eyes in the male are separated at the posterior corners by about twice the width of the ocellar tubercle. The front becomes much wider at the antenna and is a little wider than either eye at this point. Antennae widely separated and removed from the eye margin by no more than the length of the first two antennal segments. The oral recess occupies only the lower fourth of the head and is almost entirely ventral in position. It forms a long, triangular opening, quite narrow anteriorly and not very wide posteriorly. The gena is demarcated laterally by a longitudinal tentorial fissurelike crease. It occupies about half the space from the eye to the inner wall of the oral cnp. The head from above shows that the occipital lobes are very tightly apposed and the fissure quite shallow. From it arises some scaliform pile.

Thorax: Thorax a little longer than wide, gently convex, feebly shining, largely blackish over the mesonotum with the entire lateral margin including the humerus, the entire scutellum, and 2 medial vittae in front of the scutellum yellowish or reddish brown. Pile over the middle of the mesonotum scanty, short, flat-appressed, more or less flattened. Lateral pile longer and much more dense and subappressed or even a little matted. None of this lateral pile is of any great length. The anterior collar of pile forms an erect band of moderately long, stiff hair becoming shorter posteriorly. There are no bristles anywhere on mesonotum or scutellum. The mesopleuron and upper sternopleuron, and

upper half of pteropleuron, each have considerable comparatively long, stiff pile. Also the metapleuron in front of the haltere has much long, dense pile over almost its entire surface. There is a tuft of long, flattened hair beneath the base of the haltere, another tuft above the posterior coxa. Metanotum extremely short, apparently bare, greatly overhung by the scutellum. Halteres quite small. Squama with a fringe of long scales.

Legs: Entirely yellow and quite weak. All the femora are short and slender and covered with fine, rather closely appressed, sharp, black setae. In addition the hind femur bears 3 or 4 oblique, fine, short bristles on the posteroventral margin. Anterior tibia smooth, except for 3 or 4 dorsal, small, flat-appressed setae. The front tarsi are quite short, anterior claws without pulvilli. The middle tibia has 4 rows of very fine, sharp, small, black bristles, 4 or 5 in each ventral row and 6 or 7 in each dorsal row. Hind tibia similar, the dorsal bristles smaller and appressed. The anterodorsal margin with 20 or more closely adjacent, small, oblique, short, black bristles. Hind tarsi short, the claws scarcely bent even at the apex, yellow at the base, black at the apex and without pulvilli. Hesse (1956) notes that the basal tooth of the claw is very much reduced, short and spinelike.

Wings: Uniformly tinged with light yellowish brown. There are 3 submarginal cells. The anterior branch of the third vein arises quite rectangularly, cuts halfway across the second submarginal cell before dividing it into two. The united branches of the second and third vein make a very strong rectangular bend, and the first submarginal cell has the shape of a "foot." The anterior crossvein arises at the middle of the discal cell and the second vein arises gently or sometimes almost rectangularly just in front of this crossvein. The discal cell is of curious shape. It is deeply occluded through the middle by a long, rectangular branch from the lower division of the medius; this rectangular vein has a backward spur. Anal cell widely open. Axillary lobe large. The wing is wide at the base, but the alula is rather slender and elongate oval. Ambient vein complete. Basal comb of the costa exceptionally wide. The basal spur is prominent.

Abdomen: Short, oval, and obtuse, as wide as the thorax and 7 tergites are visible in the male. The first tergite laterally bears an appressed, scanty, fringe of long, pale, bristly pile; middle of the dorsum of the abdomen covered especially along the posterior borders of the tergite with flat-appressed, blackish scales and some pale scales laterally. Moreover, pale scales and hair predominate on the last two tergites and form a conspicuous fringe on the posterior margin of the sternites. Male terminalia prominent, extruded, directed obliquely and diagonally downward and not symmetrical in position.

Hesse states "that the hypopygium differs from that of most forms of *Evoprosopa* in having the beaked apical joints hook-shaped, the slender beak curved up-

wards and outwards and its apex not bifid, is indented or notched."

Material available for study: A pair of the type-species kindly furnished through the courtesy of Dr. A. J. Hesse.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Atrichochira inermis* (Bezzi), 1912 (as *Exoprosopa*); *pediformis* (Bezzi), 1924 (as *Exoprosopa*).

Genus *Diatropomma* Bowden

FIGURES 194A, 199, 404

Diatropomma Bowden, Journ. Ent. Soc. South Africa, Pretoria, vol. 25, no. 1, p. 116, 1962. Type of genus: *Diatropomma carcassoni* Bowden, 1962, by original designation.

Diatropomma Bowden consists of comparatively small *Exoprosopa*-like flies in which the base of the largely blackish wing, with midposterior clear spot and tinged apex, is rather strongly narrowed. This reduction of the axillary lobe and alula is shared by *Isotamia* Bezzi and these flies differ from that genus and also from *Exoprosopa* Macquart by the distinct pubescence of the eyes, visible at low magnification. Bowden observes that the form of the genitalia, the short, stiff pubescence, form of discal cell, and the sharp upward bend of the anterior branch of the third vein all ally this fly to the *Heteralonia* Rondani or the *Acerodisca* Bezzi groups within the Exoprosopinae.

Only 2 species are known, the type-species from Kenya, and *claudia* François from Urundi.

Length: 7.8 to 10.1 mm., wing 9.9 to 11.3 mm., proboscis 2.3 to 2.8 mm.

One can find nothing to add to Bowden's analytical comparison, which I quote:

This new genus appears to have most in common with *Isotamia* Bezzi (= *Francoisia* Hesse, *Ogilviella* (Paramonov)). With *Isotamia* Bezzi it shares several features, such as reduced axillary lobe and alula, anal cell of about equal width, short thorax, relatively bare pleura, short, stiff and blunted hairs on pleura and at base of abdomen, and also the depressed (although not grooved) face, long proboscis and indistinct genal grooves. It differs conspicuously from *Isotamia* Bezzi and *Exoprosopa* Macquart in the distinct pubescence of the eyes (although not previously reported, many species of Bombyliidae possess microscopic pubescence on the eyes, which is usually only visible in good light at high magnification, whereas in *Diatropomma* Bowden the pubescence is easily visible at low magnification), the peculiar structure of the third antennal segment, the greatly reduced fringes to the squama and alula and the remarkable development of cilia all round the wing. The genitalia of the male are unremarkable, except that the aedeagal sheath is considerably broadened and rounded apically, and are generally reminiscent of species of *Heteralonia* Macquart or *Acerodisca* Bezzi rather than other subgenera and species groups within *Exoprosopa* Macquart. This relation is further suggested by the sharp upward bend of R_{2+3} , the form of the discal cell, head structure and to a certain extent the short stiff pubescence. The general appearance of the type species also suggest a *Heteralonia* Rondani or

a species of *Defillipia* Lioy such as *consanguinea* Macq. or *aigerrima* Bezzi.

As I have not seen material of *Diatropomma* Bowden, I quote his description in full:

Body with vestiture generally reduced and sparse; thoracic hair in collar, along notopleura and on pleura, as well as that in lateral tuft of first abdominal segment, stiff, short and coarse. Head with occiput about level with vertex, occipital pit deep but occipital cleft more or less closed; ocellar tubercle set well forward of vertex; frons of approximately equal width in both sexes; eyes with small indentation and weak bisecting line, with equal facets and with very short, sparse but quite distinct pubescence; face conically produced, somewhat depressed medially and indented at apex, genal furrows almost obliterated; antennae with third segment stout, with a small conical apical sub-segment which bears a minute apparently sclerotized cap; under high magnification third antennal segment densely hairy; proboscis long, projecting well forward of face; palpi slender only slightly shorter in length than antennae.

Thorax: Short relative to scutellum, barely twice length of latter, and broad, quite distinctly broader than long; humeral calli prominent, postalar calli not or barely marked off from disc of thorax and represented by projecting posterior angles of notum; meso- and metapleural sclerites relatively prominent, particularly the latter, plunula sparse; scutellum broadly rounded; thoracic bristles well developed, especially postalar bristles, scutellar weaker.

Abdomen: Long and narrow; bristles greatly reduced, absent except for extreme sides and small ones at apex. Legs with fore coxae long, little shorter than fore femora (excluding trochanters); fore femora, tibiae and tarsi subequal, the fore legs thus relatively unmodified, fore femora without bristles, fore tibiae with well developed and numerous spicules; tarsi with strong ventral bristle rows, fore tarsi also with some longish hairs in both sexes; claws of fore tarsi less markedly reduced than in *Exoprosopa* Macquart, other claws well developed and all with a blunt basal tooth; pulvilli absent.

Wings: Long relative to body, markedly pedunculate, axillary lobe reduced and linear, about as wide as anal cell; alula reduced, lobelike; squamae much reduced, auriform; basal comb small; R_{2+3} arising in a smooth obtuse curve at about or slightly beyond r-m, the latter slightly before middle of discal cell which is relatively long, apical vein of discal cell short, regularly S-shaped, more or less parallel to wing margin; first posterior cell widely open, second and third posterior cells of equal width at wing margin, anal cell of approximately equal width throughout, widely open at wing margin; cilia of costal margin extending right round wing, becoming longer at base of axillary lobe and on alula, which is without scales; squamae with sparse narrow scales and also with some bristly hairs at angle with alula; wings conspicuously infusate with an extensive pattern like that of *Littorhynchus* Macquart, which has, in type species, a prolongation into second submarginal cell and a subsidiary, less intense, apical infusation separated from main infusation by a narrow hyaline band; hyaline or subhyaline fenestrae present over main bifurcations and cross veins. Hypopygium with basimeres long, subquadrate; telomeres long and narrow, with a reflexed apical point; aedeagus short and slender, ventral aedeagal processes (aedeagal sheath) large, broadly rounded; paraphyses broad, relatively pointed at apices, apodeme simple.

Material available for study: None. I have had to rely upon Bowden's description and excellent illustrations.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record. Bowden states that it seems to be at home in the semiarid country of the Rift Valley.

Distribution: Ethiopian: *Diatropomma carcassoni* Bowden, 1962; *claudia* (François), 1960 (as *Exoprosopa*).

Genus *Heteralonia* Rondani

FIGURE 194

Heteralonia Rondani, Arch. Zool. Anat. Fisiol., vol. 3, p. 57, sep., 1863. Type of genus: *Exoprosopa oculata* Macquart, 1840, by original designation, as *Exoprosopa occulta* Rondani, 1863, lapsus.

A curious little fly, about 6 mm. long, that is quickly distinguished by the peculiar venation of its small speckled wing. It is black and feebly shining, the wing sepia brown obliquely on the anterior half with still darker spots on all crossveins, vein furcations and additional spots near the posterior margin. There are 3 or 4 submarginal cells, and the first submarginal cell is closed and stalked and has a peculiar shape.

An erect, plane, rectangular crossvein can be interpreted as by Bezzi (1924) as dividing the marginal cell into two parts, or as by Hesse (1956) as constituting an extra oblique crossvein dividing the anterior, apical, submarginal cell into two parts. Both the two known species show this peculiarity constantly. Hesse suggests that since a somewhat similar situation exists in *Ligyra* Newman, there is adequate basis for leaving *Heteralonia* Rondani a separate genus; with this view I am inclined to agree. It is possible to interpret all of these so-called crossveins as normal branches of the radial system.

Two species are known, one from Senegal and Ghana, another from South West Africa.

Length: 6 to 8 mm.; wing 6 to 9 mm.

Head, lateral aspect: The head is hemiglobular but peaked in front on account of the triangular, conical face. The occiput is comparatively short, both at the vertex of the head and also at the bottom of the head. Dorsally the occiput is convex near the eye margin, but rapidly curved vertically downward so that it has not much thickness at this point and the medial fissure is vertical. At the bottom of the head, however, the occiput slopes very gradually backward, and it is also produced distinctly below the eye, and bears chiefly pollen on the bottom, but on the middle and dorsal part of the occiput there is a matlike cover of rather dense, flat-appressed, outwardly directed yellowish scales. The eye rises abruptly and conspicuously above the occiput on the dorsal half of the eye. The eye is reniform, the posterior indentation deep and extensive above and below with a rather pronounced, bisecting line between the eye facets at the bottom of this indentation. The front is slightly raised, very convex in profile, pollinose over a black ground color, with scattered, strong, erect or curled, bristly hairs, those at the vertex longer than the first antennal segment.

The face is conically or triangularly produced forward as a not quite equilateral triangle. The pile of the

face is similar to that of the front, bristly or long setate, rather strongly appressed, also black in color and with the long, bristly setae forming a fringe, overlapping the edge of the oral recess; the elements are somewhat stouter in the middle of the face. There are also a few, appressed, golden scales. The proboscis is rather short, extending barely beyond the oral recess. It is slender with long, slender, pointed labellum. Palpus small, cylindrical and short with a few, stiff hairs below and laterally. The antennae are attached at the upper third of the head. The first segment is widened apically with very short setae dorsally and laterally and a few ventrally. This segment is about twice as long as the basal width. The second segment is beadlike, wider than long. The third segment is elongate and conical. At the apex of the cone it bears an articulated, slender style, bristle-tipped, the style no longer than the remainder of the segment.

Head, anterior aspect: The head is a little wider than the thorax, circular, the eyes separated in the male by a distance scarcely more than the length of the first two antennal segments. Female vertex slightly wider. A rather unique feature appears to be the extreme forward position of the small, low, isosceles ocellar tubercle which lies distant from the posterior eye margin at least one-third the length of the front. Posterior eye corners rounded and the eye facets of uniform size. The antennae are separated widely and are distant from the eye margin by less than the length of the first segment. Face and oral cup narrow, the latter is triangular. Posteriorly behind the proboscis, the oral cup is thin-walled and moderately deep, but this only begins midway along the sides. Anteriorly the wall is inflated and thickened with rounded instead of sharp edge and this thickened area reaches to half of the anterior division of the oral recess. Gena linear. The oral cup is moderately produced downward from the eye margin.

Thorax: Almost quadrate, but a little narrowed across the anterior margin. Humerus swollen with numerous, long, black, bristly hairs. Surface of mesonotum and scutellum shining with faint pollen and scattered, fine, sparse, erect hairs, and scattered, flat-appressed setae above the wing and more widely on the scutellum. Notopleuron with some short, stout, black bristles. Postalar callosity with 3 or 4 long, slender, black bristles and the scutellar margin with 3 or 4 pairs of more slender, black bristles. Mesopleuron with a bushy tuft of very stiff, black, blunt, bristles or bristly hairs. Anterior collar composed of similar elements, but rather short. The anterior pteropleuron has a tuft of bristly hairs. The sternopleuron has some appressed, bristly hair and long, bristly hairs, very dense on the metapleuron. Hypopleuron bare. No tufts of pile beneath the haltere.

Legs: The legs are comparatively short and stout, but not swollen. The anterior tarsi has strongly appressed, short, stout setae. Middle femur with some long, slender bristles. There are 2 in the middle on the front side, 3 shorter ones posteriorly. The middle

tarsus has some rather conspicuous, though slender, bristles, which are few in number. There are 3 antero-dorsal and 2 or 3 posterodorsal bristles. The hind femur bears 4 moderately long, slender bristles anteroventrally and 2 dorsally at the apex. Its tibia also has the bristles scanty. There are 4 or 5 anterodorsal bristles, the same number anteroventrally, and 5 or 6 posterodorsally. Claws long, slender, sharp, slightly curved toward the apex and with a distinct, basal tooth.

Wings: Comparatively large, considering the small size of the fly, slender, with a characteristic dark sepia, ocellated pattern in spots especially on the crossveins and becoming confluent anterobasally. There are 3 submarginal cells and 2 marginal cells. The shape of the second submarginal cell is peculiar. It is somewhat scapulate, extending as far basally from the base of the first submarginal cell as it does outward into the first submarginal cell. First posterior cell strongly narrowed at the apex. Anal cell open almost maximally. Wings slender at the base, the axillary lobe comparatively narrow, the alula narrow, the ambient vein complete. The costal comb narrow, and the costal hook thornlike.

Abdomen: Longer than the thorax and distinctly though not greatly wider. It is shining black, narrowly oval, and densely covered with flat-appressed, slender, scaleform black pile and considerable amounts of brownish-yellow wider scales. There are a few, scattered, fine, sparse, black hairs along the lateral margin, and subapically on the last tergite. Posterior margins of the sternites with similarly slender, somewhat more numerous hairs. Male terminalia moderately large, visible from the sides or below, conical and thrust toward the left of the insect. More in evidence from below, the lateral margin of most of the tergites and posterior edge of the last tergite have a conspicuous single row or fringe of short, broad, black scales.

Material available for study: The type-species presented to me through the courtesy of Mr. John Bowden.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no record of adult behavior.

Distribution: Ethiopian: *Heteralonia kaokoensis* Hesse, 1956; *oculata* (Macquart), 1840 (as *Exoprosopa*) [= *cosmoptera* Bezzi, 19—].

Genus *Isotamia* Bezzi

FIGURES 193, 402, 684, 688

Isotamia Bezzi, Trans. Ent. Soc. London, p. 627, 1912 (1911).

Type of genus: *Isotamia daceyi*, by original designation.

Francoisia Hesse, Bull. Inst. Sci. nat. Belgique, vol. 28, no. 42, p. 1, 1952. Type of genus: *Francoisia sulcifacies* Hesse, 1952, by original designation.

Ogilviella Paramonov, Proc. Roy. Ent. Soc. London, (B), vol. 23, p. 26, 1954b. Type of genus: *Ogilviella tridentata* Paramonov, 1954b, by original designation.

These are peculiar, comparatively small flies, which are rather bare; they have short scales on head, thorax, and more abundantly upon the abdomen. The slender,

basally narrowed wing, has 3 submarginal cells, and a sharply delimited irregular anterior, blackish pattern superficially very much like some species of *Anthrax* Scopoli. The third vein arises, however, well before the anterior crossvein, and while obtuse at its origin it is not rectangular. The third antennal segment is conical with long, slender apex and in addition a long terminal style. The proboscis is long and slender; posterior eye margin is indented together with short bisecting line; occiput only moderately tumid or conspicuous but with a deep central cavity. Anterior and middle tibiae with weak spicules, hind tibia with somewhat more prominent ones; hind femur with 3 spines below near apex; pulvilli absent.

Though placed by Bezzi in the Lomatiinae, I agree with Hesse concerning its true relationship within the Exoprosopinae. It differs from *Exoprosopa* Macquart by the reduced axillary lobe and alula, less pile on pleuron, less reduced front claws, dorsal groove-like depression of the face, short palpus, long proboscis, and stiff, stout, bristly pile on pleuron and base of abdomen.

Known from a single species found in central Africa.

Length: 7 to 8 mm.; wing 9 mm.

Head, lateral aspect: The head is hemispherical. The face is rather conspicuous and angularly produced; however, since it is demarcated laterally and obliquely by a crease running just inside the antenna to the eye margin, and this crease or sulcus is continued transversely across just below the antenna, possibly the extended portion should properly be regarded as part of the oragenal cup. The oragenal cup is deep but narrow, divergent below with the outer margin sharply marked but with the walls thick and expanded on each side. Gena virtually absent, confined to an indistinct groove near the eye at the lower part of the eye. The pile of the face consists of flat-appressed, minute, broad and quite short scales. There are 2 shallow, central depressions on the front, 1 over the middle and 1 above the antenna. Also, there is a curious, V-shaped depression in the middle at the oral margin. The sides of the front and the middle of the face and sides of the oragenal cup each have a few, scattered, stout, short, oblique setae. Occiput only moderately developed but a little longer above though slanting backward and it is also bilobate with a narrow fissure. On the lower half the eye extends farther backward and also the occiput extends farther downward behind the proboscis. The occiput has a large, central cavity bordered with abundant, short, erect pile. The remainder and anterior portion is covered with small, appressed, scattered scales. The palpus is moderately long and slender with long, slender, setate hairs laterally, especially toward the base.

The proboscis is quite long and slender and about twice as long as the head. The antennae are attached near the upper fourth of the head or slightly beneath it; they are minute, the first segment is nearly twice as long as the second and bears above and below a few fine setae; second segment with some shorter setae dorsally and 1 or 2 setae below. The third segment is strongly

and triangularly bulbous at the base, abruptly drawn out into a slender, stylelike portion only as long as the basal part; it bears an equally slender style which is a little longer than the length of the 3 segments combined and likewise has a microscopic spine at the tip.

Head, anterior aspect: The head is as wide as thorax, the female vertex is very little more than half the width of the front at the antenna. The antennae are quite widely separated, and separated from the eye margins by less than the width of 1 segment. The ocellar tubercle is small and so shallow as to be almost absent; the shallow, convex ridge, however, is creased laterally and extends backward to the lobes of the occiput.

Thorax: The thorax is short and broad, the scutellum quite wide but rather short and without strongly developed posterolateral angles. The mesonotum is shining black, the scutellum likewise, both covered with moderately abundant, flat-appressed scales, some of them minute, most of them moderately large. The anterior margin of the mesonotum has a narrow band of coarse, pale yellow, erect, bristly pile of moderate length changing to black on the swollen, protuberant humerus on its outer portion. Notopleuron with some short bristles, postalar callosity with 3 or 4 longer, slightly stouter, tuberculate bristles. Scutellar margin with 2 or 3 slender, not very long, black bristles. There is a conspicuous tuft or band of long, moderately stout, black bristles upon the upper margin of the mesopleuron and the more anterior elements are better developed, the greater, lower part of the mesopleuron bare. The upper pteropleuron has a few setae; upper metapleuron above the haltere and in front of it with a tuft of numerous, long, slender, black bristles; hypopleuron bare; the squama has only a very few fine, short hairs on it, and no scales.

Legs: The legs rather slender but comparatively short, they bear scattered, flat-appressed, dark scales, and also scanty, minute, appressed setae. The hind femur has 2 long, stout spicules below and 1 smaller and 1 or 2 others dorsally on each side near the apex; anterior tibia has 2 or 3 minute spicules dorsally. The hind tibia, however, has 3 or 4 conspicuous spicules especially below and also 5 or 6 shorter ones above; there are 4 rows altogether. The tarsi are quite short, the claws small, pulvilli absent.

Wings: The wings are rather long and slender and characteristically greatly narrowed toward the base. The alula is absent or reduced to a narrow, thickened fold. There are 3 submarginal cells, the anal cell is quite widely open, the basal vein anteriorly on the third posterior cell is undulate, the anterior crossvein enters the discal cell beyond the middle and the second vein arises a considerable distance proximal to the anterior crossvein by 2 or more times the length of the anterior crossvein. The anterior half of the wing is blackish sepia, irregularly but sharply demarcated; base of costa without conspicuous setae but there is a sharp, spinelike lobe.

Abdomen: The abdomen is moderately elongate, not quite twice as long as the thorax but broader than the

thorax and with nearly parallel sides to the end of the sixth segment. Abdomen shining black, covered with conspicuous, pale, broad, flat-appressed scales, which are apt to be largely denuded and with some black scales intermixed especially along the posterior margin of the sixth and seventh tergites where they extend out free and are broad and conspicuous. The sides of the first tergite have a dense band of moderately long, erect, coarse, black pile which, however, does not appear to extend under the scutellum in the middle of the segment. Sternites with scales only.

Material available for study: Type of *Ogilviella tridentata* Paramonov in the British Museum (Natural History).

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Ethiopian: *Isotamia daveyi* Bezzi, 1912 [= *sulcifacies* (Hesse), 1952 (as *Francoisia*), = *tridentata* (Paramonov), 1954 (as *Ogilviella*)].

Genus *Litorrhynchus* Macquart

FIGURES 191, 408, 687, 689

Litorrhynchus Macquart, *Diptères exotiques*, vol. 2, pt. 1, p. 78, 1840. Type of genus: *Bibio lar* Fabricius, 1781. Designated by Oldroyd, 1940, as type by remainder and correction of error in Coquillett, 1910.

Litorrhynchus Bezzi, *The Bombyliidae of the Ethiopian Region*, p. 3, 1924, emendation.

Coquillett (1910, p. 562) designated *Litorrhynchus hamatus* Macquart, the second of 4 species, as type-species. Coquillett did not realize that 3 of the species Macquart included—*Anthrax senicentus* Wiedemann, *A. collaris* Wiedemann, and his own new species *L. hamatus*—were as shown by Loew (1860) and by Ricardo (1901) actually equivalent to *Exoprosopa*, *sensu stricto*.

Bezzi (1924), pp. 212-214, key to 25 Ethiopian species.

Hesse (1956), pp. 625-631, key to 16 South African species.

While dipterists at the National Museum of Natural History suggest that I change the name *Litorrhynchus* Macquart to read *Litomyza*, new name, because of strict adherence to the rules, I strongly believe the purpose of taxonomy is ill served by changing a name in use for 130 years. I decline to do so, hence I leave the fixation as Oldroyd made it 100 years after the naming of the genus.

Large, beautiful flies related to *Exoprosopa* Macquart and generally with a handsome and very characteristic pattern of brown or yellow or both colors on the wing. Bezzi, who in 1912 redescribed the genus and in 1924 commented upon it further, emphasized the rounded face, with longer proboscis extending beyond the oral cavity. Bezzi particularly called attention to the long, sharp, basal tooth on the claws, shared by *Exoprosopa* Macquart, and also the spicules present on the anterior tibia. Bezzi admitted that some species of *Exoprosopa* Macquart do have front tibial spicules, and he noted that a few species like *ignara* Loew have a similar wing pattern; see also *decipiens* Bezzi, *curvicornis* Bezzi, and

ptersticha Hesse. The very different American genus *Stonyx* Osten Sacken likewise has a basal tooth on the claw, but a different wing pattern and other differences. While admittedly there is some overlapping of characters, it is at once apparent when comparing a number of species that *Litorrhynchus* Macquart constitutes a rather unique group within the tribe Exoprosopini and that this genus should be restricted to those *Exoprosopa*-like flies that combine blunt, rounded face with tooth on the claws, spicules on the anterior tibia, and characteristic wing pattern. The very rounded face alone will usually separate them from the species of *Exoprosopa* Macquart, which have a conically pointed face.

Macquart in erecting this genus noted that the Indian species *Biblio lar* Fabricius from the Orient was to be included within the genus and contained its characters; but then he also assigned to it a South African species and another Oriental species both of which subsequently proved to be true members of the genus *Exoprosopa* Macquart in the strict sense. Oldroyd (1940) chose the only sensible course and designated the Indian species *lar* Fabricius as the type-species; this species differs slightly from the African species. I have illustrated *lar* Fabricius through the courtesy of Mr. Oldroyd and also have been able to study a number of African species through the courtesy of Dr. A. J. Hesse.

Litorrhynchus Macquart is a characteristic element of the bee fly fauna of that part of Africa lying below the equator. Bezzi (1924) keys 25 species and treats 18; Hesse (1956) treats 16 species.

Length: 6.5 to 18 mm., more commonly 10 to 12 mm.; wing 9 to 22 mm.

Head, lateral aspect: The head is subglobular with strongly developed and tumid occiput and the face, while it is moderately prominent, is broadly rounded. The face extends a little farther outward than the length of the first two antennal segments; it is characteristically bluntly rounded as compared with the conical face of *Exoprosopa* Macquart; the oragenal cup is narrow, but deep, except in front, its walls are much widened or thickened and rounded with the surface pollinose. The pile of both face and front is abundant, yet not dense. It is fine, erect, stiff, and rather short with a considerable number of long, flat-appressed scales intermixed. The posterior eye margin very shallow and broadly concave, but at the middle it has a short, bisecting line. The occiput is about as long as the face at its greatest length. The pile is short and erect giving away along the eye margins to a rather broad border of quite dense, matted, or flat-appressed, usually pale scales. The occiput behind the ocelli is bilobate; the fissure is quite narrow since the lobes are touching. The palpus has 1 segment, is quite long and quite slender with numerous, rather long, slender, bristly hairs on the ventral surface, shorter ones above. The proboscis extends distinctly beyond the oral cavity. The nonoral part of the genae is exceptionally narrow, the crease is deep but the sides close.

The antennae are attached at the upper third of the head, the first segment is longer and may be about twice as long as the second and 3 or 4 times as large. It bears numerous, moderately long, coarse, bristly setae on all sides, except the upper half of the medial surface, which is more or less bare. Third segment either conical or clublike, its base broader and more bulbiform; this segment is often long; terminally it ends in a slender, apically dilated stylelike segment, itself bearing an apical spinelet.

Head, anterior aspect: The head is as wide as the thorax, the female vertex is only half as wide as the front at the base of antennae and the ocellar tubercle quite low and undeveloped. The small ocelli are set in a short isosceles triangle. The front is relatively smooth but may be slightly swollen in the middle. The oral opening is narrow, rapidly widening at the base of the proboscis.

Thorax: The thorax is short and broad and only slightly convex. The scutellum is quite large, the mesonotum tends to have rather dense, flat-appressed, often shining, scaliform pile in which, however, are intermixed some subappressed, quite fine, posteriorly directed hairs. Anterior margin of the mesonotum with a conspicuous fringe of long, slender, erect, dense, pale bristles. The humerus is sharply swollen and often bears both black and yellow bristles. Notopleuron with 2 or 3 rather long, conspicuous, stout bristles and anteriorly a row of shorter bristles. Postalar callosity with 2 or 3 quite stout, conspicuous bristles and several more slender ones. Margin of the scutellum with 6 to 8 pairs of rather stout, moderately long bristles, which tend to be curved across one another in the middle. The disc bears abundant, fine, suberect pile and some yellow scales or scaliform pile, flat-appressed especially on the base. Squama with a fringe of broad, often brownish scales. Almost the whole of the mesopleuron is covered with dense, coarse, bristly or wiry pile often of 2 colors, the upper, coarser, more bristly pile is longer, directed upward and the pteropleuron especially posterodorsally has a large, subappressed clump of coarse, bristly pile. Metapleuron with dense, erect, long, coarse pile on a vertical band down its middle. Also, there is a tuft of pile at the base of the halteres below. Hypopleuron bare. Propleuron with tufts of long pile on each side.

Legs: The legs are relatively short and stout, especially the femora. Anterior femur swollen from base to near the apex. The pile consists of dense, large, broad, flat-appressed scales together with minute, fine, appressed, setate hairs. The pile of the tibiae is similar but the setae are finer and more appressed, the scales perhaps smaller. The hind femur has 2 lateral spicules but none below. The anterior tibia has a posterodorsal row of 8 or 9 quite small spicules and a few much smaller spicules anteriorly, also a few much more slender posteroventral spicules. The spicules on the hind tibia are appressed and moderately well developed with about 10 to 12 in each row; claws rather sharp but slender with a basal tooth; pulvilli absent.

Wings: The wings are large and tending to be a little longer than the fly. They are apt to have a very characteristic pattern of sepia brown, or reddish brown and yellowish brown with some fenestrate spots and the apex often hyaline as well as a posterior triangular spot in the middle. The discal cell is broad with the second posterior cell wide toward its base. Base of costa with well developed comb of bristles and with a sharp, long, hooked or beaklike process.

Abdomen: The abdomen is comparatively long oval but quite broad across the first two tergites and shallowly oval. The ground color is apt to be light brown, reddish or yellowish and the surface is covered densely with scales that are mostly dark but sometimes these are intermixed with scales or patches of scales that are opaque white, and there are also considerable, short, fine, strongly appressed, bristly hairs. The female terminalia bear a row of curved spines on each side. The male terminalia, according to Hesse, have a crest of dense hairs or spiny hairs dorsally in apical part of each basal part; distimeres (beaked apical segments) slightly curved outward and up, the apex of each ending in a slightly longer, upper, outer, curved hooklike point and in a lower, inner, shorter, blunt process; each distimere has a prominent, raised, blunt, projecting process on the outer side just before middle of joint; the aedeagus has a prominent, ventral, scooplike process which usually forms a broadened apical, central keel; the aedeagus has a prominent, ventral, scooplike process which usually forms a broadened apical, central keel; the aedeagus itself is short; lateral struts shaped much as a shoe horn; posteriorly projecting strut racket-shaped.

Dr. A. J. Hesse in his work on South African bee flies describes the male hypopygium as follows:

Hypopygium of males with a crest of dense hairs or sometimes almost spine-like hairs along dorsal part in apical half of each basal part; beaked apical joints slightly curved outwards and upwards, the apex of each ending in a slightly longer, upper, outer, curved, hook-like point and in a lower, inner, shorter, blunter process; each beaked apical joint also with a prominently raised, blunt, projecting process on outer side just before middle of joint; aedeagal apparatus with a prominent, ventral, scoop-like aedeagal process, which is usually broadened apically and centrally keel-like on dorsal aspect (side view); aedeagus itself relatively short; lateral struts of middle aedeagal part strongly developed, broadly shoe-horn-shaped; posteriorly projecting strut chopper-shaped or racket-shaped.

Material studied: The series in the British Museum (Natural History) and an example of the type-species lent by this museum. Dr. A. J. Hesse kindly sent several species from South Africa for dissection and study.

Immature stages: One species has been bred in South Africa from the mud nests of a wasp. See comments under life histories.

Ecology and behavior of adults: Very few notes are on record. Hesse (1958) notes that they appear more abundantly in grass-steppe, savannah, and broken-bush country, and are not common in the Karoo and arid types of country; he says the wing pattern, striking

when in open grass veldt, renders them almost invisible in the shadows of broken thornbush.

Distribution: Ethiopian: *Litorrhynchus argyrolepis* Bezzi, 1912; *atricapillus* Hesse, 1956; *basalis* (Ricardo), 1901 (as *Exoprosopa*); *bechuanus* Hesse, 1936; *corticeus* Bezzi, 1924, *corticeus corticalis* Bezzi, 1924; *damerensis* Hesse, 1956; *dentifer* Bezzi, 1912; *dilatatus* Bezzi, 1912; *ectophaeus* Hesse, 1956; *erythraeus* Bezzi, 1906, *erythraeus allothyris* Bezzi, 1923; *fuscatus* Bezzi, 1924; *kaokoensis* Hesse, 1956; *macropterus* (Loew), 1860 (as *Exoprosopa*) [= *longipennis* Loew, 1863 (as *Exoprosopa*) (no descr.), = *tollini* Bezzi, 1924, not Loew]; *maurus* (Thunberg), 1827 (as *Tanyglossa*) [= *collaris* Macquart, 1840, not Wiedemann, *erythraea* Speiser, subg. *Exosoma*, = *rostrata* Loew, 1860]; *metapleurialis* Bezzi, 1924; *nyasae* Ricardo, 1901 [= *argyrolepis* Bezzi, 1921, in part]; *obumbratus* Bezzi, 1924 [= *macropterus* Ricardo, not Loew]; *perplexus* Bezzi, 1912; *phloeochromus* Bezzi, 1922; *productus* Bezzi, 1924; *pseudocollaris* Bezzi, 1924 [= *maurus* Bezzi, 1921, in part]; *repletus* Bezzi, 1912; *ricardoi* Bezzi, 1912; *rostratus* (Loew), 1860 (as *Exoprosopa*); *siccifolius* Bezzi, 1924; *suberosus* Bezzi, 1924; *suspensus* Bezzi, 1924; *tollini* (Loew), 1863 (as *Exoprosopa*); *vernayi* Hesse, 1956 [= *nyasae* Hesse, 1936, not Ricardo].

Oriental: *Litorrhynchus lar* (Fabricius), 1781 (as *Bibio*).

Genus *Micomitra* Bowden

FIGURES 203, 421, 694

Micomitra Bowden, Mem. Ent. Soc. Southern Africa, Pretoria, no. 8, p. 147, 1964. Type of genus: *Exoprosopa parvicellula* Bezzi, 1921, by original designation.

The genus *Micomitra* Bowden was erected to contain a group of species of South Africa *Exoprosopa* Macquart, sensu lato, which displayed a combination of characters not found among other species. According to Bowden they show a shining integument, generally brilliantly shining, iridescent scales on several parts of the body, greatly reduced chaetotaxy, much more reduced than in other *Exoprosopa* species, and with thoracic bristles especially weak or wanting. Also Bowden points out that the males have U-shaped telomeres and greatly expanded ventral aedeagal process.

This genus contains the species that were included by Bezzi (1924) in his *stupidus* Rossi group, and by Hesse (1956) in his *parvicellula* Bezzi group. They have the wings completely hyaline, shining and iridescent, even without infuscation basally or in the costal cell. First posterior cell usually broadly open according to Hesse, with the integument of the frons shining. Like the *Acrodicea* and *Heteralonia* groups of *Exoprosopa* the ocelli are set rather far forward. Note that the antennal style of the third antennal segment is minute and spinelike. Also the species are of small size, rarely exceeding 10 mm. in length. Bezzi noted the slight

development of the basal tooth on the claw, the short wings without praediscoidal spot.

Micomitra is distributed through the Mediterranean and Ethiopian regions, more abundantly in South Africa. Bowden placed 12 species here: *parvicellula* Bezzi (type-species), *stupidia* Rossi, *iris* Loew, *famula* Bezzi, *chrySTALLINA* Bezzi, *pharao* Paramonov, *bella* Austen, *iridipennis* Hesse, *opalina* Hesse, *perlucida* Hesse, *aerata* Hesse, and *anthracina* Bowden. Bezzi included *serva* Bezzi, *erronea* Bezzi, *brachycera* Bezzi, *ancilla* Bezzi, *chionea* Bezzi, and *latissima* Bezzi.

Length: 5.5 to 11 mm.; wing 4.8 to 9 mm. Most species less than 10 mm.

Head, lateral aspect: Semiglobular, the face bluntly triangular, forming almost a rectangle with the oragenal cavity. The face is covered with broad, iridescent, pale scales which are flatly plastered against the surface. Continued narrowly down the sides of the gena and with a few short, very fine, quite erect, white hairs anteriorly on the gena. Face and gena and the basal segments of the antenna often pale yellow. There may be a few minute setae medially on the peak of the face. The occiput is quite prominent, rounded, and sloping to the eye margin, plastered over the flat or tightly appressed silvery scales and the large central cavity bearing a short fringe around its border. Occipital lobes tightly apposed. Posterior eye margin broadly but deeply indented below the middle and with a bisecting line in the facets. The upper facets are twice as large as the ventral ones. The palpus is slender, but short, cylindrical, with a few fine hairs tending to be curved and less than half as long as the proboscis. The proboscis is rather short, often directed straight forward, but not extending farther than the oragenal recess. It is strongly compressed laterally with microspinules ventrally which are arranged in rows. The labellum is also compressed, a little more than twice as long as wide, a little pointed apically, and a little widened when viewed from above.

The antennae are attached just above the middle of the head. They are small with the first two segments nearly equal, the third is longer than the first two segments combined; its width at the base equal to that of the short second segment and beyond the base it is progressively attenuate to the apex. The apex consists of an extremely small, short, slender, articulated micro-segment.

Head, anterior aspect: The head is distinctly wider than the thorax, very globular when viewed from above. The oragenal recess is quite narrow and deep, both above and below, widened posteriorly where the proboscis emerges. The walls of the oragenal recess are widened and strongly sloping outward and also backward to the eye margin. They are only slightly inflated medially just below the middle. There is a long, sharp, tentorial fissure separating the quite narrow gena throughout its length. The antennae are very widely separated and removed from the eye margin by less than the thickness of the first segment. The eyes in the male

are very narrowly separated behind the ocelli by the thickness of one ocellus. The ocellar tubercle is prominent, though small and is set rather far forward from the posterior eye corner. The male front rapidly widens to form a rather wide isosceles triangle completely covered with wide, iridescent, silvery, obliquely appressed scales that completely obscure the black ground color. This dense mat of scales ends abruptly between and opposite the first antennal segment. The first antennal segment bears some very short, fine white pile in the species *opalina* Hesse.

Thorax: The thorax is distinctly longer than wide, gently convex, feebly shining-black, with a few scattered broad, coppery scales in *opalina* Hesse, completely flat-appressed. The anterior collar is composed of dense, long, erect, shining white pile, and there is a lateral border of dense, matted, opaque, white pile on the sides of the metanotum and the anterior postalar callosity. This callosity is set apart by a deep medial crease. The scutellum is large but only gently convex, subtriangular in shape with a few slender, white bristly hairs along the margin and a deep basal crease. The mesopleuron has a dense mat of long, opaque, white pile dorsally extending backward over the pteropleuron. Only the ventral margin of the pteropleuron has a few scattered, white hairs. Posteriorly the sternopleuron has some green scales in *opalina* Hesse. It is set apart along the middle by an angular ridge, leaving the upper part depressed and concave. The hypopleuron is bare, and there is a small tuft of pile on the metapleuron above the spiracle. Above the posterior coxa is a dense mat of appressed silvery scales in *opalina* Hesse. Squama with a dense border of opaque, white pile.

Legs: The legs are comparatively short. The hind pair are, however, longer. The middle and posterior femora are stout without being conspicuously thickened or swollen. They bear broad, appressed, white scales and the hind femur especially has a few, fine, scattered, appressed, black setae. The hind tibiae are much longer than the hind femora and have several rows of oblique, numerous black setae. Claws slender; the basal tooth is quite short; pulvilli absent. The arolium is stublike. Anterior tibiae without spicules. The tarsi are quite short.

Wings: The wings are completely hyaline, strongly iridescent. The anterior veins are pale yellow, the posterior veins are light brown. The second vein arises abruptly but not rectangularly just beyond the anterior crossvein. The anterior crossvein is rectangular entering the discal cell a little before the middle. There are 3 submarginal cells. The first and third are equally wide at the base; the marginal cell is a little expanded and rounded posteriorly apically. Apically the discal cell is expanded anteriorly, slightly narrowing the first posterior cell, and the discal cell is apically pointed and drawn-out distally. The intercalary vein is parallel with the wing margin; the second and third posterior cells are equally long on the wing margin and the third posterior cell is angulate and plane basally and ante-

riorly but without spur veins. Anal cell widely open, axillary lobe wide; the alula twice as long as wide and the ambient vein complete. The costal comb is broad and conspicuous with microsetate hairs; there is a small spinelike spur at the extreme base.

Abdomen: Abdomen is elongate, as long as thorax and scutellum combined, rather convex, with 7 tergites visible from above. In *opalina* Hesse it is shiny black with numerous, small, metallic, black scales and large very wide, flat-appressed, white scales, which tend to form a conspicuous anterior border on the third tergite, extending also onto the base of the second and more widely and conspicuously on the last two tergites. Sternites with conspicuous anterior or posterior borders of white scales. Male terminalia exposed ventrally and twisted to the right. Hesse in describing the male terminalia of this group of species, which were included by Bowden in his genus *Micromitra* Bowden, notes that the male of *opalina* Hesse is very similar to that of *iridipennis* Hesse and *parvicellula* Bezzi, differing from both in having the apical angle of basal parts distinctly more angular and not rounded; basal strut neither broad nor very narrow; posterior processes of aedeagal complex distinctly much shorter; lateral apical angles of ventral aedeagal process more spinelike than in *parvicellula* Bezzi.

Material available for study: Through the generosity of Dr. A. J. Hesse I have received a male of *opalina* Hesse for dissection and study.

Immature stages: Unknown.

Ecology and behavior of adults: Not on record.

Distribution: Palaearctic: *Micromitra aerata* Hesse, 1956; *ancilla* Bezzi, 1924; *anthracina* Bowden, 1964; *bella* Austen, 1937; *brachycera* Bezzi, 1924; *chionea* Bezzi, 1924; *chrysellina* Bezzi, 1924; *erronea* Bezzi, 1924; *famula* Bezzi, 1923; *iridipennis* Hesse, 1956; *iris* Loew, 1869; *latissima* Bezzi, 1924; *opalina* Hesse, 1956; *parvicellula* (Bezzi), 1921 (as *Exoprosopa*); *perlucida* Hesse, 1956; *pharao* Paramonov, 19—; *serva* Bezzi, 1924; *stipida* Rossi, 1790 [= *chalcoides* Pallas in Wiedemann, 1818, = *rhodamanthus* Meigen, 1804, = *vitreicosta* Walker, 1849], *stipida pharao* Paramonov, 1928, female.

Colossoptera, new genus

FIGURES 201, 418, 714, 969, 970

Colossoptera, new genus. Type of genus: *Exoprosopa latipennis* Brunetti, 1909, by present designation.

An *Exoprosopa*-like fly with extraordinarily large, extensive, broad wing, of uniform sepia brown color; readily mistaken at first sight for *Cyananthrax* Painter, they have articulated antennal style and 3 submarginal cells, as in *Exoprosopa* Macquart. The wings dwarf the elongate, parallel-sided abdomen. The third antennal segment is tiny, but the style is long and slender. The first posterior cell is narrowly yet distinctly open. The

third posterior cell on the wing margin is 3 times, or more, as wide as the second posterior cell on the margin; there are no spur veins. Face conical.

Found in northern India.

Length: 16 mm.; wing 19 mm.; abdomen 10 mm.; its width 4 mm.

Head, lateral aspect: Head hemiglobular; the occiput is moderately prominent, wider above than below, and strongly sloping inward. The pile is flat-appressed and consists of narrow scales; the central fringe is short. The eye is reniform, the indentation broadly rounded, extensive above and below, and the eye is bisected at the middle posteriorly. The front is a little swollen, arising above the eye margin, and not any more extensive at the antenna than it is in the middle. The pile of the front is bristly, erect, and black, and the front is opaque black with dark brown pollen. There are a few pale, scattered scales on the lower front and few on the face. The face is triangularly produced forward, but not acutely peaked. It bears considerable erect bristly pile, concentrated medially at the apex and forming a fringe down the sides of the oral recess. The proboscis and labellum are slender, only a little longer than the oral recess, the palpus slender, nearly half as long as the proboscis with a few long, stiff hairs below. The antennae are attached just above the middle of the head and are rather small. First segment is cylindrical, $2\frac{1}{2}$ times as long as wide. Second segment quite bead-like, as wide as long with rounded sides, narrowly attached to the third segment. The first segment bears some long bristly setae or short bristles on all sides, except below. The second segment has minute setae. The third segment is small, forming an elongate, attenuate cone, nearly as long as the first segment, nearly plane on all sides and with a segmented style a trifle longer than the segment.

Head, anterior aspect: Circular, wider than the thorax. The ocellar tubercle is minute, abrupt, slightly longer than wide, and with the space between the eyes at least $4\frac{1}{2}$ times as great as the width of the ocellar tubercle. The antennae are widely separated by nearly the length of the first three segments and separated from the eye margin by little more than half the length of the first segment. The oral recess is long and slender with thickened sloping walls on the anterior half; it is shallow posteriorly and not enclosing the proboscis or palpus. Genal space very narrow. The tentorial crease is long and very narrow. Gena a little more extensive beneath the eye perhaps. The occipital lobes are tightly apposed.

Thorax: Subquadrate and small, opaque black with brown pollen. The pile of the mesonotum consists of very fine, erect, blackish hairs becoming longer in front of the scutellum, with a narrow, anterior collar of deep yellow pile continued over the whole of the humerus and with tufts of pile continued laterally along the sides of the mesonotum, yellow and matted and long, with a conspicuous tuft over the wing and on the postalar callosity. Scutellum clothed like the mesonotum. Pleu-

ron black with brown pollen, the pile black, except dorsally. The upper mesopleural pile and the dense pile of the metapleuron is long and yellow. The pteropleuron also bears some blackish pile. The sternopleural and propleural pile is all brownish black. Hair tuft beneath the halteres apparently absent. Squamal scales slender. There are 3 quite stout, long, black bristles on the notopleuron, 4 or 5 on the postalar callosity; the margin of the scutellum has only fine long hairs, the plumula with yellow hairs, the humerus with a rather sharp lateral spur.

Legs: Slender and long. Anterior tibia nearly smooth. Middle femur with several stout bristles anteriorly along the middle. Hind femur with a double row of long, slender, distinct bristles ventrally, 7 bristles ventrolaterally. There are 3 or 4 other long, fine hairs, also 6 ventromedial. Also there are several additional long hairs distally, and 5 bristles anterodorsally on the outer half. All the femora and tibiae with numerous, flat-appressed, shining, brownish-black scales. The long hind tibiae have slender bristles placed in 4 rows; there are 9 ventrolateral, 18 dorsolateral, and 10 or more dorsomedial, besides 10 ventromedial. All tarsi spiculate below. Anterior claws slightly reduced. Other claws long, sharp, slender, slightly bent at the apex, and with a strong, long, basal tooth.

Wings: Very large and broad, giving this fly the appearance of the genus *Cyananthrax* Painter, for which I first mistook it. The wing is uniformly dark sepia brown, unrelieved by spots or windows and without a thyridial fleck. The venation is a little peculiar. There are 3 submarginal cells. The first submarginal cell is strongly drawn-out toward the base of the wing, and the anterior branch of the second vein is strongly sigmoid, and the posterior branch is also sigmoid. The first posterior cell is narrowed apically. The second posterior cell is much narrowed, leaving the third posterior cell very wide on the margin. Medial crossvein with a double bend, one at the base and one at the apex. The very long, upper anterior intercalary vein is also bent at each end. Contact of the discal cell with the fourth posterior cell short, and shorter than the anterior crossvein; this crossvein enters the discal cell before the middle and the second vein arises opposite the anterior crossvein. Alula narrow. Ambient vein complete. Costal comb narrow, the hook long and sharp.

Abdomen: Abdomen elongate; it is nearly 3 times as long as the mesonotum if the scutellum is excepted. Color black, more or less shining, with faint pollen, the sides of the second and third tergites a little yellowish. The abdomen bears numerous, flat-appressed, black scales with some yellow scales laterally, and it also bears conspicuous, coarse, matted, straw-yellow, long, backwardly appressed pile on the sides of the abdomen, except the last tergite which has only black. There are 7 tergites visible. The last one has a fringe of bristly black hair laterally and posteriorly. Male terminalia large, the dististyli extruded posteriorly.

The male terminalia from dorsal aspect, epandrium removed, show a short, oval structure with quite wide, tongue-like or shovel-like epiphallus. The base of the aedeagus is pear-shaped, rather wide basally. From the lateral aspect the basistylus is stout, especially basally; it is more than twice as long as wide; it is bluntly rounded apically, with the dististyli rising quite subapically. The epiphallus is prominent; the epandrium is sharply triangular, more or less rectangular dorso-basally, but hooked back at that angle, and with a very prominent extensive, attenuate lobe turned downward basally.

Material available for study: The unique type.

Immature stages: Unknown.

Ecology and behavior of adults: Unknown.

Distribution: Oriental: *Colossoptera latipennis* (Brunetti), 1909 (as *Exoprosopa*).

Genus *Ligyra* Newman

FIGURES 192, 202, 425, 704, 731, 962, 963

Ligyra Newman, Entomologist, vol. 1, no. 14, p. 220, 1841. Type of genus: *Anthrax bombyliiformis* MacLeay, 1827, by monotypy.

Hyperalonia Rondani, Arch. Zool. Anat. Fisiol., vol. 3, p. 58, 1863. Type of genus: *Stomoxys morio* Fabricius, 1775, as *Anthrax erythrocephala* Fabricius, 1805. Designated by Coquillett, p. 554, 1910, the 5th of 13 species. In this work regarded as a subgenus.

Velocia Coquillett, Canadian Ent., vol. 18, p. 158, 1886b. Type of genus: *Anthrax cerberus* Fabricius, 1794, by monotypy. Preoccupied by Robineau-Desvoidy, 1863.

Ligira, of Authors.

Bezzi (1924), pp. 361-363, key to 19 Ethiopian species (as *Hyperalonia*).

Roberts (1928a), p. 96, key to 9 Australian species (as *Hyperalonia*).

Paramonov (1929a), pp. 188-189, comments on the *venus* Karsch group (as *Hyperalonia*).

Engel (1936), pp. 455-456, key to 6 Palaearctic species (as *Hyperalonia*).

Paramonov (1953a), pp. 220-222, comments on the *venus* group (as *Ligyra*).

Hesse (1956), pp. 914-917, key to 10 Ethiopian species (as *Ligyra*).

Bowden (1964), p. 151, key to 5 West African species (as *Ligyra*).

Paramonov (1967), pp. 124-127, key to 22 known species from Australia (as *Ligyra*).

Painter (1968), pp. 107-121, review of *Hyperalonia* Rondani, segregates as a separate South American genus.

Large robust flies which cannot be effectively distinguished from *Exoprosopa* Macquart except in the constant presence of 4 or more submarginal cells and the short, blunt tooth at the base of the claw. The wing is usually long; sometimes extraordinarily long and slender as in the *venus* Karsch group of species from South Africa. In other species it is broad as in *kaupii* Jaenicke.

The wings show a striking pattern of sepia brown, sometimes a very dark color, and in some species the base of the wing, the costa, and subcostal cells are yellow.

lowish. There are many types of wing patterns such as that of *chilensis* Rondani, *proserpina* Wiedemann, *bombyliiformis* MacLeay, *gazophylax* Loew, *tantalus* Fabricius, *venus* Karsch, and *atricosta* Bezzi; each is different. Species groups can be more effectively grouped around the type of venation, which varies in several particulars; but more especially the discal cell; this cell in one group is long or short, strongly constricted below in the middle, in another group it is lengthened and pointed at the apex, in a third group, wide and obtuse at apex with the closing vein rather long. The anterior crossvein usually enters the discal cell at the middle, but in *venus* Karsch and a few others it enters before the middle. The shape of the anal vein offers useful specific characters. Unfortunately, even when taken with other characters such as the relative width and length of the wing and the abdominal and leg vestiture, there is so much overlapping of species that species groups still remain ill defined.

In Chile they extend as far south as Araucania, but are common at the latitude of Concepción. These species were relegated back to *Hyperalonia* Rondani by Painter (1968).

I regard the basal crossvein dividing the submarginal area as being the anterior branch of the third vein, meeting the posterior branch of the second vein in partial confluence and then departing for the edge of the wing.

In species of *Exoprosopa* Macquart the posteriorly directed branch closing the upper half of the third submarginal (basal) cell has often been regarded as a crossvein (sectorial vein); I believe a more accurate interpretation is to regard it as the posterior branch of the second vein meeting the anterior branch of the third vein; in support of this I point out that it is strongly oblique in many species. The additional transverse veins found in *Ligyra* Newman, always one, sometimes two, may be regarded as remnants of extra veins similar to those found in the Nemestrinidae. In any case since *Exoprosopa* Macquart shows more simplified venation, *Ligyra* Newman must be regarded as more generalized and ancient in type; the former genus more successful, more recent, with far wider distribution.

Length: Body 10 to 20 mm.; width of body 5 to 8 mm.; length of wing 10 to 24 mm.; width of wing 6 to 7 mm.; wing spread 24 to 56 mm.; in *L. venus* Karsch the wing is 6 mm. wide and 25 mm. long.

The genus *Ligyra* Newman differs so little from *Exoprosopa* Macquart that a detailed and lengthy description would merely duplicate the description of the latter genus in nearly every particular. I have therefore chosen to comment on the genus in only general terms and include remarks on distribution and species groups.

Head, lateral aspect: Similar to *Exoprosopa* Macquart. The proboscis is contained within the oral recess or projects only a short distance beyond it except in *albiventris* Macquart where it is twice as long. There appear to be numerous specific differences in the orna-

mentation of the proboscis and labellum in the species before me. The face is bluntly conical in all species with which I am acquainted except *L. chilensis* Rondani and *albiventris* Macquart where it is bluntly rounded but protuberant. Antenna similar to *Exoprosopa* Macquart.

Head, anterior aspect: Oragenal recess narrow, inflated in the middle, the inflated part usually rounded, sometimes ridged.

Thorax: Similar to *Exoprosopa* Macquart. Disc of mesonotum rarely with scales. Bristles of notopleuron strong, variable in number; stout and long on the post-alar callosity.

Legs: Like *Exoprosopa* Macquart. Anterior tibia usually smooth, more rarely spiculate. Hind legs at least with scales except in *chilensis* Rondani. Tooth at base of claw very short, scarcely discernible in some species; always blunt.

Wings: Similar to *Exoprosopa* Macquart in size, shape and frequency of strong patterns of brown or black. Constantly different from *Exoprosopa* Macquart in the presence of 4 or sometimes 5 submarginal cells. Costa strongly expanded at base.

Abdomen: Similar to *Exoprosopa* Macquart. Scales present on the abdomen in most species. Female terminalia with spines on each side near apex. Hesse (1956) notes that the genitalia do not differ much from those of *Exoprosopa* Macquart in the structure and shape of the dististyli and the aedeagal process.

Bezzi (1924) and Hesse (1956) recognized the following groups of South African species:

1. The *Ligyra nigripennis* Loew group

Wings relatively broad. Venation rather similar to *Litorrhynchus* Macquart or *Exoprosopa* Macquart, subgenus *Defilippia* Lioy. Discal cell of characteristic shape, the constriction lying below the anterior crossvein and the upper part of the distal extremity, elongate, rounded, pointed at apex; wings uniformly infuscated, in color yellow brown, brown or even purplish, cell middles paler. Third antennal segment relatively short and more conical, the style longer than half the length of the segment. Abdomen and legs with yellow or golden scabose pile.

Species included: *vittata* Ricardo, *niveifrons* Bezzi, *evanida* Bezzi, *helena* Loew, *paris* Bezzi, *coleoptrata* Bezzi, *nigripennis* Loew, and according to Bezzi the Oriental species *tantalus* Fabricius, *leucanoe* Jaennicke, *oenomus* Rondani, and *chrysolampis* Jaennicke.

2. The *Ligyra sisypus* Fabricious group

Wings narrower than in the preceding group and the general coloration of the legs and body more reddish. Wings varying from hyaline to others with a much reduced brown or yellow pattern narrowly restricted to the foreborder or occasionally with broad crossbands. Venation of these species quite different, the discal cell

regular, not strongly constricted in the middle, the apex wide and nearly or quite plain, not pointed and elongated; vein between second and third posterior cells nearly straight.

Species included: *Ligyra sisypus* Fabricius, *atricosta* Bezzi, *abula* Bezzi, *virgo* Bezzi, *thyridophora* Bezzi, *doryca* Boisduval, *transiens* Bezzi.

3. The *Ligyra venus* Karsch group

Bezzi speaks of these as the most beautiful of all African Diptera; those I have seen are certainly remarkable. Wings very long and narrow with characteristic and extensive pattern of dark brown bands extending backward from the dark foreborder. Discal cell wide, gradually and particularly widened apically, its end vein oblique and a little shortened; this cell is only slightly constricted. The front tibia is spiculate and the hind legs are feathered with rather long suberect scales. Abdomen with conspicuous patches of golden scales, generally two basal, one at apex, arranged as a triangle. Head sometimes red, sometimes with collar, and notopleural pile tufts bright orange or red.

Species included: *Ligyra venus* Karsch, *cupido* Bezzi, *mars* Bezzi, *mars-vulcanus* Bezzi, *enderleini* Paramonov. This group is more tropical in its distribution and is absent from South Africa.

While I am familiar with 9 of the 14 New World species, I am not able to fit them well into the Old World species groups. The three species *hela* Erichson, *albiventris* Macquart, and *gazophylax* Loew all have such similar wing venation, wing spot pattern, and abdominal scale coloration and distribution pattern that they would seem to have a very close relationship; yet *albiventris* Macquart has a very blunt, rounded face and proboscis twice as long as the oral cavity, in great contrast to the other two species; this seems to indicate a more important and stable relationship for the wing characteristics, pattern included, than for type of face and length of proboscis.

Since Williston (1901, p. 273), and Painter (1930) point out that the Chilean group of species, *morio* Fabricius, *chilensis* Rondani, *erythrocephala* Fabricius, differs from typical *Ligyra* in lacking a segmented style, I here resurrect the name *Hyperalonia* Rondani as a subgenus to include only these three species; they are further notable for the absence of true scales and for the greatly swollen apical half of the discal cell. Painter (1930) says the metapleuron has only 1 or 2 hairs; this is not true of my material, which does not differ in this respect. This new use of the name *Hyperalonia* is apart from the erroneous use by many early authors who were unaware of the priority of *Ligyra*. I find 5 submarginal cells constantly present in *Ligyra kaupei* Jaennicke and in my material of *Ligyra tenebrosa* Paramonov.

Abdominal patterns may be characteristic; of species before me 8 have a band of pale scales at the base of the

second and rarely of the third tergite; 6 species have either apical tergites wholly pale scaloze or the last 2 or 3 tergites each with an isolated spot of pale scales on each side; *Ligyra venus* Karsch and its allies are noted for patches of golden scales at base and apex of abdomen.

The male terminalia from dorsal aspect, epandrium removed, show a figure moderately wide basally and narrowed apically. The epiphallus widens from the base to the apex where it is quite wide, barely curved at the blunt apex. Base of aedeagus bulblike and almost circular. From the lateral aspect the apically incised, hooded dististyle is small, lobelike and subapical to only a moderate extent. Epandrium distinctly triangular, but with the anterior basal margin broadly but only shallowly incised.

Prior to 1934 *Exoprosopa*-like flies with 4 submarginal cells were placed under the name *Hyperalonia* Rondani (1864). Edwards (1934) called attention to the older name *Ligyra* Newman (1841) and also to the fact that Newman in naming his genus *Ligyra* selected *Anthrax bombylifornis* MacLeay as the type-species. Hardy (1941, p. 233; 1942, p. 203) has indicated a belief that *bombylifornis* MacLeay is the same as *Bibio sylvanus* Fabricius (1787), but as Hardy can hardly have seen the Fabricius type, I feel that the statement wants confirmation. This synonymy is here adopted with reservation. *Ligyra* Newman is a genus of much fewer species than *Exoprosopa* Macquart; nevertheless, they are widespread. Two species are found in southwestern United States: *gazophylax* Loew from southern Arizona and California, which I have taken as far north as San Lucas; and *pilatei* Macquart, which occurs in Peru and extends into southern Arizona. From the Palaearctic region, species are known only from China, Japan, Formosa, India, Arabia, Egypt, Erythraea, Ussuri, and one species from Greece and the Island of Rhodes. About an equal number of species are known from the tropical part of the New World and the tropical part of Ethiopia, and a larger number than from any other area.

Material available for study: Thirteen species in my own collection together with the material in the British Museum (Natural History) and the National Museum of Natural History.

Immature stages: Hyperparasites; as far as known parasites of scollids, such as *Tiphia*, which in turn are parasites of subterranean scarabaeid larvae. See life history section for further details.

Ecology and behavior of adults: Bowden (1964) furnished some interesting observations on several species he found hovering about small clearings in scrub or hawking along the sides of hedges, hovering about buildings; he found *L. paris* Bezzi hovering about the ends of projecting branches of trees and that the species showed a strong territorial attitude, driving intruders away from its chosen spot, or returning if chased away. He found *sisypus* Fabricius to be a ground-frequenting species. The species I have taken

in California, Mexico, and Australia have all been found in stream beds resting warily upon rocks or sand.

Painter (1930) collected 2 species, *albiventris* Macquart and *latreillii* Wiedemann, flying about sandy ocean beaches in Honduras.

Distribution: Nearctic: *Ligyra gazophylax* (Loew), 1869 (as *Exoprosopa*); *pilatei* (Macquart), 1846 (as *Exoprosopa*).

Neotropical: *Ligyra albiventris* (Macquart), 1848 (as *Exoprosopa*) [= *hela* (Erichson), 1848 (as *Anthrax*)]; *cerberus* (Fabricius), 1794 (as *Anthrax*); *chilensis* Rondani, 1863; *dido* Osten Sacken, 1886; *flavosparsa* Bigot, 1892; *gargantua* Knab, 1915; *guerini* (Macquart), 1846 (as *Exoprosopa*); *kaupii* (Jaennicke), 1867 (as *Exoprosopa*); *koslowskyi* Edwards, 1930; *latreillii* (Wiedemann), 1830 (as *Anthrax*); *morio* (Fabricius), 1775 (as *Stomoxys*) [= *coeruleiventris* (Macquart), 1846 (as *Exoprosopa*), = *erythrocephala* (Fabricius), 1805 (as *Anthrax*)]; *proserpina* (Wiedemann), 1828 (as *Anthrax*) [= *cerberus* (Macquart), 1840 (as *Exoprosopa*), = *klugii* (Wiedemann), 1830 (as *Anthrax*)]; = *rufescens* (Walker), 1849, (as *Anthrax*)]; *sevrillei* (Macquart), 1840 (as *Exoprosopa*, no descr.); *sirinamensis* Rondani, 1863.

Palaearectic: *Ligyra ferrea* (Walker), 1849 (as *Anthrax*) [= *versicolor* Loew in litt.]; *flavofasciata* (Macquart), 1855 (as *Exoprosopa*); *formosana* Paramonov, 1931; *gebleri* (Loew), 1854 (as *Exoprosopa*); *helenae* (Loew), 1854 (as *Exoprosopa*) [= *gloriosa* (Walker), 1871 (as *Exoprosopa*)]; *monacha* (Klug), 1832 (as *Anthrax*); *orientalis* Paramonov, 1931; *shirakii* Paramonov, 1931; *similis* Coquillett, 1898; *tantalus* (Fabricius), 1794 (as *Anthrax*) [= *coeruleopennis* (Dole-schall), 1858 (as *Anthrax*)]; *ussuriensis* Paramonov, 1936.

Ethiopian: *Ligyra alula* (Bezzi), 1906 (as *Exoprosopa*); *atricosta* Bezzi, 1924; *coleoptata* Bezzi, 1921; *cupido* Bezzi, 1924; *mars* Bezzi, 1924, *mars-vulcanus* Bezzi, 1924; *melanoptera* Bowden, 1964; *minerva* Paramonov, 1953; *nigripennis* (Loew), 1852 (as *Exoprosopa*); *niveifrons* Bezzi, 1914; *paris* Bezzi, 1924; *sisyphus* (Fabricius), 1805 (as *Anthrax*); *thyridophora*

Bezzi, 1912; *transiens* Bezzi, 1924; *venus* Karsch, 1887 [= *enderleini* Paramonov, 1953]; *virgo* Bezzi, 1924; *vittata* Ricardo, 1901.

Oriental: *Ligyra albicincta* (Macquart), 1931 (as *Anthrax*); *argyura* de Meijere, 1924; *celebesi* Paramonov, 1931; *chrysolampis* (Jaennicke), 1867 (as *Exoprosopa*); *curvata* de Meijere, 1911; *doryca* (Boisduval), 1835 (as *Anthrax*) [= *audouinii* (Macquart), 1840 (as *Exoprosopa*), = *leuconoe* (Jaennicke), 1867 (as *Exoprosopa*), = *pelops* (Walker), 1859 (as *Anthrax*), = *ventrimacula* (Dole-schall), 1857 (as *Anthrax*)]; *enderleini* Paramonov, 1929; *evanida* Bezzi, 1920; *flavotomentosa* de Meijere, 1929; *macassarensis* Paramonov, 1931; *oenomachus* Rondani, 1875, *oenomachus flora* Frey, 1934; *paludosa* de Meijere, 1911; *semifusca* Brunetti, 1912; *sphinx* (Fabricius), 1787 (as *Bibio*) [= *imbuta* (Walker), 1849 (as *Anthrax*)]; *suffusipennis* Brunetti, 1909; *sumatrensis* de Meijere, 1911; *tantalus* (Fabricius), 1794 (as *Anthrax*) [= *coeruleiventris* (Dole-schall), 1858 (as *Anthrax*)].

Australian: *Ligyra bombyliiformis* (Macleay), 1827 (as *Anthrax*); [= *albiventris* (Thomson), 1869 (as *Exoprosopa*), = *punctipennis* (Macquart), 1849 (as *Exoprosopa*)]; *burnsi* Paramonov, 1967; *calabyana* Paramonov, 1967; *campbelli* Paramonov, 1967; *chinnicki* Paramonov, 1967; *cingulata* (Wulp), 1885 (as *Exoprosopa*); *commoni* Paramonov, 1967; *contrastata* Paramonov, 1967; *dentata* (Roberts), 1928 (as *Hyperalonia*); *doryca* (Boisduval), 1835 (as *Anthrax*); *eyreana* Paramonov, 1967; *fasciata* Paramonov, 1967; *hemifusca* (Roberts), 1928 (as *Hyperalonia*); *inquinita* (Roberts), 1928 (as *Hyperalonia*); *macraspis* (Thomson), 1868 (as *Exoprosopa*) [= *argenticincta* (Bigot), 1892 (as *Hyperalonia*), = *sinuatifascia* (Hardy not Macquart), 1924 (as *Hyperalonia*)]; *orest* Paramonov, 1967; *pilad* Paramonov, 1967; *robertsi* Paramonov, 1967; *satyrus* (Fabricius), 1775 (as *Bibio*) [= *funesta* (Walker), 1849 (as *Exoprosopa*), = *insignis* (Macquart), 1855 (as *Exoprosopa*)]; *septentrionis* (Roberts), 1928 (as *Hyperalonia*); *sinuatifascia* (Macquart), 1855 (as *Exoprosopa*); *tenebrosa* Paramonov, 1967.

Subfamily Anthracinae Latreille, 1804

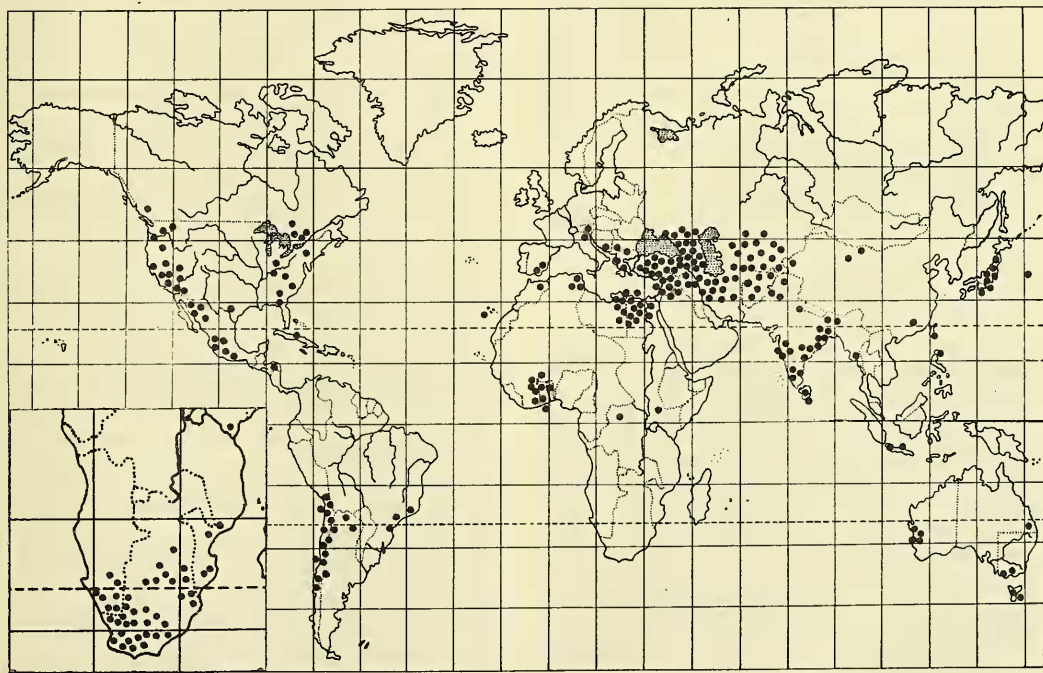
(As Anthracii)

All of these flies have a number of interesting features in common. Many species are quite large. Many, and in fact the majority, are a dull somber black relieved sometimes by spots of silver pile on the abdominal tergites or on the apex of abdomen or with a wide band of silver pile. Wings with 2 or 3 submarginal cells. The second vein arises abruptly, at a right angle, at a point located at or very near the anterior crossvein; a backward spur vein may be present. First segment of antenna always quite short; second segment likewise short. The third segment is usually strongly bulblike or onion-shaped at base with an attenuate style; how-

ever, the third segment may be conical. This style bears a rather short apical microsegment of the same thickness as the stylate part of the third segment. At the apex this microsegment bears a characteristic circlet or brush of hairs except in *Walkeromyia* Paramonov. Male genitalia large and placed symmetrically.

As pointed out by Bowden (1964), Bezzi was mistaken in thinking this group lacked spines on the ovipositor. The ovipositor does have a circlet of spines which are recessed because of the invagination of the acanthophorites. The face is always rounded, the proboscis quite short; pulvilli well developed; besides these,

ANTHRACINAE



TEXT-FIGURE 47.—Pattern of the approximate world distribution of the species of the subfamily Anthracinae.

several other characters separate this group from the Exoprosopinae. The metapleuron is constantly bare and without pile on front of the haltere and the squama has a fringe of hairs instead of scales. The male genitalia are large and placed symmetrically. It appears to be connected to the Lomatiinae through the tribe Xeramoebini.

The question arises as to what genera may be properly included in this subfamily and what should be left in the Lomatiinae. It is the opinion of the author that *Chionanoeba* Sack, *Petrorossia* Becker, and *Xeramoeba* Hesse should remain in Lomatiinae; perhaps also *Prothaplocnemis* Bezzi; in these genera the second vein does indeed arise rather abruptly and at a varying distance from the fork of the third vein; the face is short, the proboscis short, but so it is in *Aphobantus* Loew. These features may be parallel developments rather than annectent relationships. And so I restrict the Anthracinae to *Anthrax* Scopoli (together with cer-

tain subgenera), *Dicranoclista* Bezzi, and the curious and aberrant *Walkeromyia* Paramonov.

The distribution is interesting. *Anthrax* Scopoli is of worldwide distribution; *Walkeromyia* Paramonov is found in Trinidad and also the Chilean subregion and is practically a phylogeront or relict type; *Dicranoclista* Bezzi is found in central Africa and the southwestern United States.

Based on the North American species I have dissected, the genus *Anthrax* Scopoli shows a structure in which the epandrium is extraordinarily long and rather slender with a downturned basal lobe itself long and prominent and suggestive of a condition often seen in both the Exoprosopinae and the Lomatiinae. There may be a short, blunt lobe in the Bombyliinae but never a long slender lobe; the basal stylus also is peculiar, it is quite wide at the base, long, slender, and narrowed apically. The epiphallus extends well beyond the dististylus, and this structure is narrowed in the middle.

KEY TO THE GENERA OF THE ANTHRACINAE*

1. Wings with 2 submarginal cells, the second having a basal spur. Third antennal segment long, conical, gradually tapered from the base, the separated microsegment has reduced apical hairs and with apical spine, or the hairs even sometimes absent or denuded. Face below antenna more than usually extensive due to the shortened, reduced oral recess and shortened proboscis. Face very blunt and bulbose. Very large flies; in the male the long hind legs bear an extraordinary fringe of quite long scales extending from the outer third of the hind femur to the second tarsal segment *Walkeromyia* Paramonov
2. Third antennal segment very loosely attached to the second segment. Wings with 2 submarginal cells. Anterior branch of third vein with or without a spur vein.

Anthrax Scopoli

- Third antennal segment very tightly apposed and joined to the second segment. Wings with 3 submarginal cells; rarely with 2 3
3. Three submarginal cells formed below by a supernumerary crossvein as in *Ligyra* Newman, the base of anterior branch of third vein with a long basal stump vein, and origin of second vein likewise with a stump vein. First posterior cell closed and bearing a long stalk. No scales or bristles on abdomen *Dicranoclista* Bezzi
- Three submarginal cells formed above by extension of the stump vein at base of anterior branch of third vein. No supernumerary crossvein below. First posterior cell open. (*Argyramoeba* of authors). The subgenus *Spogostylum* in the Macquart sense.

Anthrax (*Spogostylum*) Macquart

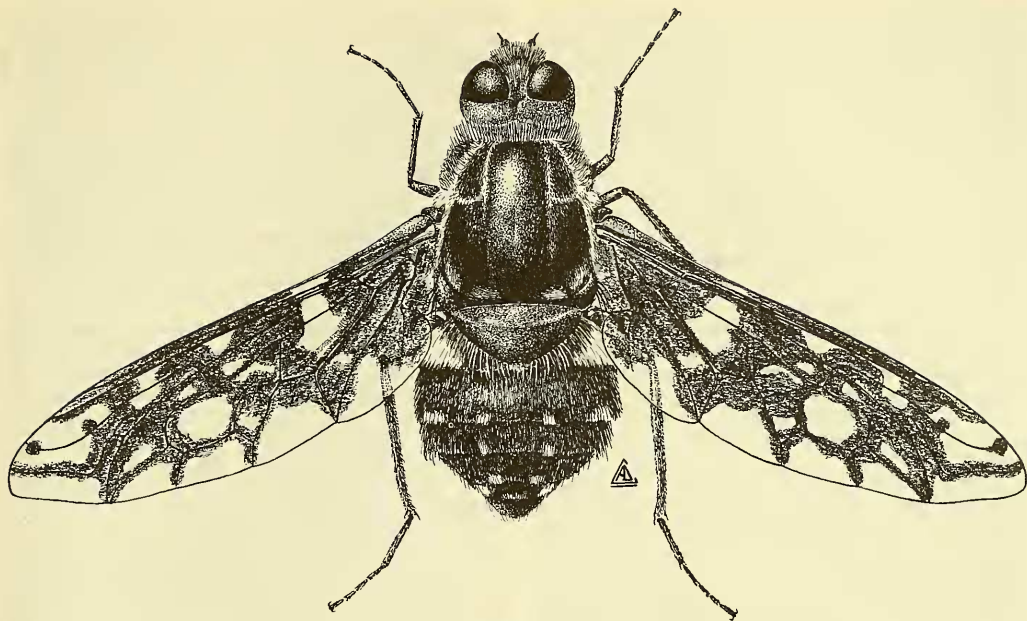
* See also *Coniomastix* Enderlein (Pamirs, Central Asia).

Genus *Anthrax* Scopoli

FIGURES 159, 160A, 163, 337, 409, 712, 734, 966, 967, 968

- Anthrax* Scopoli, Entomologia Carniolica, p. 358, 1763. Type of genus; *Musca anthrax* Schrank, 1781 (misident. as *Musca morio* Linnaeus, 1758). See Aldrich, 1926, p. 12.
- Chalcamoeba* Sack, Abhand. Senckenberg. Naturf. Ges., vol. 30, p. 522, 1909. Type of genus: *Anthrax virgo* Egger, 1859, by original designation.
- Chrysamoeba* Sack, Abhand. Senckenberg. Naturf. Ges., vol. 30, p. 522, 1909. Type of genus: *Chrysamoeba vulpina* Sack, 1909, by original designation.
- Leucamoeba* Sack, Abhand. Senckenberg. Naturf. Ges., vol. 30, p. 520, 1909. Type of genus: *Bibio aethiops* Fabricius, 1781, by original designation.
- Molybdamoeba* Sack, Abhand. Senckenberg. Naturf. Ges., vol. 30, p. 519, 1909. Type of genus: *Anthrax tripunctata* Wiedemann in Meigen, 1820, by original designation.
- Psammatamoeba* Sack, Abhand. Senckenberg. Naturf. Ges., vol. 30, p. 536, 1909. Type of genus: *Anthrax isis* Meigen, 1820, by original designation.
- Satyramoeba* Sack, Abhand. Senckenberg. Naturf. Ges., vol. 30, p. 517, 1909. Type of genus: *Anthrax etrusca* Fabricius, 1794, by original designation.

- Spogostylum* Macquart, Diptères exotiques, vol. 2, pt. 1, p. 53, 1840. Type of subgenus: *Spogostylum mystaceum* Macquart, 1840, by monotypy.
- Spongostylum* Williston [not Macquart], Manual of North American Dipt., edition II, p. 65, 1896 (emendation).
- Argyramoeba* Schiner, Wien. Ent. Monatschr., vol. 4, p. 51, 1860. Type of genus: *Musca anthrax* Schrank, designated by Sack in 1909.
- Argyramoeba* E. and L. Coucke, Ann. Soc. Ent. Belgique, vol. 38, p. 286, 1894 (emendation).
- Coquillett (1894), p. 95, key to 18 species (as *Argyramoeba*).
- White in Hardy (1924), pp. 76-77, key to 3 species (as *Argyramoeba*).
- Bezzi (1924), pp. 160-161, key to 12 Ethiopian species.
- Bezzi (1924), pp. 168-169, key to 11 Ethiopian species (as *Spongostylum*).
- Séguy (1926), pp. 205-206, key to 9 species from France.
- Engel (1936), pp. 422-424, key to species.
- Engel (1936), pp. 439-440, key to species.
- Austen (1937), pp. 109-110, key to 3 species from Palestine (as *Anthrax*).
- Austen (1937), pp. 114-115, key to 8 species from Palestine (as *Spongostylum*).

TEXT-FIGURE 48.—Habitus, *Anthrax tigrinus* DeGeer.

Hesse (1956), pp. 366-384, key to 42 male and 44 female species (as *Anthrax*).

Hesse (1956), pp. 384-387, key to species.

Paramonov (1957), pp. 126-148, key to 19 species.

Bowden (1964), p. 81, key to 6 species from Ghana (as *Anthrax*).

Bowden (1964), pp. 87-88, key to 5 species from Ghana (as *Argyramoeba*).

Osten Sacken (1886), pp. 100, key to 8 species (as *Argyramoeba*).

Marston (1970), key to all New World species except *albofasciatus* group.

Dull black flies, which are sometimes feebly shining. These are usually medium sized flies. Many species are rather large; a few are small. Quite commonly the species show a striking wing pattern of sharply delimited spots of varying number. Still others have only the anterior margin more or less black, and in a few species the wing is almost entirely hyaline or tinged with pale yellow. All species are characterized by a divided style, which bears upon the apex of the terminal section a characteristic circlet or brush of hairs arranged about an often blunt or truncate tip. All species likewise bear the following group characteristics: metapleuron in front of halteres bare, face short and rounded and proboscis always short, squamae with a fringe of hairs but no scales, etc.

Probably no genus in the family Bombyliidae, with the possible exception of *Exoprosopa* Macquart, has been involved in as much confusion. Many diverse views and opinions have been given with regard to its limitations and what should be included within it. Nevertheless there is a small base of sensible conclusions upon which to build.

This genus is worldwide in distribution, with an immense number of species for the Palaearctic and Ethiopian regions.

Length: 4 to 20 mm.

Anthrax Scopoli as the oldest name cannot be abandoned. Its type is *anthrax* Schrank, misidentified as *Musca morio* Linnaeus. It is curious that Sack (1909) overlooked *Anthrax* Scopoli in his excellent paper. *Anthrax anthrax* Schrank has 2 submarginal cells; the anterior branch of the third vein arises rectangularly, bends rectangularly, and has a well-developed backward spur which is never complete; the second vein also arises rectangularly, bends rectangularly, and has a backward spur. All species that have the above combination of characters unquestionably belong to *Anthrax* Scopoli. Beyond this point there are certain aspects of variability in the characters found within the group.

Argyromoeba Schiner has as its type, *Musca anthrax* Schrank, clearly designated by Sack in 1909, a year be-

fore Coquillett selected *Anthrax tripunctata* Wiedemann. It is then an exact synonym of *Anthrax* Scopoli and further use is invalid. Also the wing of *Anthrax tripunctata* Wiedemann (Engel, 1936, fig. 113) is identical in venation with *Anthrax anthrax* Schrank; since Sack designated *tripunctata* as the type of his *Molydamoeba*, this likewise becomes a synonym of *Anthrax* Scopoli, sensu stricto.

Beyond the above characterization one may quite reasonably ask what characters are available for further subdivision of *Anthrax* Scopoli, sensu lato, and into which group of such characters does the type-species fall.

There are two choices: First, the venation of the wings. If we are correct in assuming that the trend of wing specialization is in the main toward simplification, then we must consider the reduction from 3 submarginal cells to 2 such cells to be in the direction of simplification; and second, those species with constant spur (base of posterior branch of second vein atrophied) may be reckoned intermediate. Each of these conditions might well form the basis for further subdivision. In those species without a rectangular bend at base of second vein, or fork of third vein, where the origin of these veins are evenly rounded out, we have the basis for useful species groups.

It may be noted that there are at least three species in the Eurasian area with 3 regularly complete submarginal cells: *ocyale* Fabricius, *flavescens* Sack, and the latter is the type of *Anthraxamoeba* Sack, a name that might well be used for the species with 3 submarginal cells provided it can be demonstrated to be different from *Spogostylum* Macquart, a South American species which Bezzi (1924) notes has the submarginal cell divided in quite a different way from that of the three above-named species. The type-species of *Spogostylum* Macquart (*Spogostylum* of authors) is *mystaceum* Macquart and not *tripunctatum* Wiedemann as given by Engel (1936). It is not possible to completely change the definition of *Spogostylum* Macquart as Engel has done. Hence I reserve a decision as to the disposition of *Spogostylum* Macquart until sufficient material is available to determine (1) the manner of subdivision of the submarginal cell, (2) the regularity of the presence of 3 submarginal cells, and (3) the type of structure of the third antennal segment. Provisionally, either *Spogostylum* Macquart or *Anthraxamoeba* Sack is available for species with 3 submarginal cells; but not *Argyro-moeba* Schiner because of this synonymy given above, as it is an exact synonym of *Anthrax* Scopoli. For this reason I have had to reject the use Hesse (1956) has made of this name. I prefer to leave *Anthrax* an unsplit group with many species groups, pending a worldwide study of *Anthrax* Scopoli, in the wide sense.

Apart from the venation of *Anthrax*, sensu lato, a rather creditable attempt has been made to split up this large assemblage on the basis of the form of the second and third antennal segments and their manner of attachment. Unfortunately it is applied with some difficulty.

These two types consist, first, of those species in which the third antennal segment, at its rounded base, projects a little ways outward beyond the apex of the second segment which correspondingly is a little rounded on its outer margins, the two segments not fitting closely together, and second, the group in which these two segments fit closely into one another; this second arrangement is the cup-shaped attachment described by Bezzi, and it was made the basis for the separation of a group of species by both Bezzi and Engel under the name *Spogostylum* (emendation of *Spogostylum* Macquart). This interpretation cannot be supported until such time as adequate material of Macquart's type-species is available.

There have been efforts to split *Anthrax* species still further upon the basis of wing pattern, abdominal coloration, and shape of the stylate part of the third antennal segment (*Satyramoeba* Sack); it does not seem to me profitable to divide each possible section further, inasmuch as such a course would be tantamount to creating a separate genus for each species group.

In any case, for the present, I relegate all of these distinctions to the status of species groups within the genus *Anthrax* Scopoli, sensu lato.

Head, lateral aspect: The head is nearly globular with the occiput strongly developed backward especially on the upper half of the head. The occiput is even more prominent in the middle because of the deep indentation which is quite broad with both upper and lower angles nearly equal. There is a distinct bisecting line on the posterior eye facets. The pile of the occiput is scanty and consists of fine appressed hairs or scales or both: the circular fringe about the interior cup is short and dense. Some species have special tufts of scales along the eye margin. The front is convex, very little swollen and uniformly covered in most species with dense, long, bristly hair. However, in some *Anthrax* species the bristly pile is concentrated in patches of more dense character and there may be numerous appressed scales mixed in with the pile. The face is short and convex, pollinose, and vertically it may extend down the head as much as the length of the third antennal segment. There are a few species in which the face is slightly though bluntly protuberant beneath the antenna. There is a characteristic, conspicuous, transverse band of dense, black, bristly pile above the oral recess and the immediate area beneath the antennae is apt to be bare of pile, and these bare areas may meet in the middle and extend outward almost to the eye margin. The eye is reniform because of the deep indentation posteriorly.

The proboscis is always quite short, the labellum equal to half the length of the proboscis, long oval, but comparatively thin. The proboscis is confined to the oral recess. Palpus rather small and slender and short with a few long, bristly hairs at the apex. The antennae are attached at the middle of the head. The first two segments are quite short; the first segment is twice as long as the second and with a circular fringe of bristly

hairs on all sides in several rows. The second and third segments are either closely attached together or may be disclike with the adjacent ends of each segment rounded so that the area of attachment is reduced, and generally speaking in this latter situation, the rounded base of the third segment is apt to be extended outward, making this segment wider than the second segment. The third segment varies greatly in shape. Generally it is strongly constricted near the base, leaving an onion-shaped appearance, with abruptly narrowed style, divided into a terminal microsegment of varying length. There are other species, however (subgenus *Satyramoeba* Sack), in which the third segment is drawn out into a long tapered cone. All species of *Anthrax* Scopoli have at least a small microsegment at the apex of the third segment which bears a brush or circlet of hairs.

Head, anterior aspect: The head is more narrow than the thorax in some species such as *pluto* Wiedemann, but in the *gideon* Fabricius group it is fully as wide as the thorax. The eyes are separated in both sexes by a distance 3 times as great as the ocellar tubercle. The ocellar tubercle is quite small and obtuse. The antennae are widely separated and are rather closer to the eye margin than they are to each other in some species, in others equally spaced across the face. The oral opening is small, quite ventral in position and divided into a quadrate portion bordered by a narrow flangelike production of the gena. The gena itself is either moderately wide or linear. The sides of this part of the oral recess quite deep and vertical and this lateral ridge or wall abruptly descends interiorly so that there is a wider transverse or semicircular excavation beneath the lower margin of the face into which the labellum fits. This anterior recess has three deep, longitudinal grooves or troughs. Tentorial fissure on each side deep. Viewed from above the occipital lobes are tightly apposed and have a deep, longitudinal fissure behind the vertex.

Thorax: The thorax is slightly narrowed anteriorly, widest on the posterior half, opaque or feebly shining black or brownish black and the mesonotal pile consists of sparse, fine, short, erect, scattered hairs over the disc which in some species may be comparatively dense and the pile is longer and more abundant laterally from the humerus to the postalar callosities. This pile may be soft, matted and appressed, and even somewhat curled, but more commonly it consists of stiff, erect, bristly hairs. Bristles on the mesonotum vary from a few, weak, short bristles on the notopleuron to some species which have comparatively long, moderately stout bristles. The anterior collar of pile is distinct and may consist of only 1 or 2 rows of stiff, long hairs or may be widened into a distinct band of pile. Scutellum clothed like the mesonotum. The marginal bristles are long or short, but slender in character. Mesopleuron with much coarse, stiff pile, especially on the upper half. Pteropleuron covered densely with stiff pile. The hypopleuron and the entire metapleuron in front and behind the haltere are bare. Metanotum extremely short. Squama with a fringe of hairs.

Legs: Legs well developed. The anterior pair is only slightly smaller than the middle pair. Anterior tibia with a double row of 12 or 14 slender bristles and about the same number of short, slightly stouter bristles, posteroventrally. Anterior femur with a few slender bristles basally. Middle tibia and legs similar with 4 rows of bristles on the tibia, somewhat stouter in character and the anterodorsal with fewer elements. Hind femur stout but not swollen with an anteroventral row of stiff, sharp, pointed bristles, which may contain as few as 4 or 5 on the outer half, or 10 or 12 reaching nearly to the base. The hind tibia is stout and may have only the same number and character of bristles as on the middle tibia. In *Anthrax tigrina* De Geer the anterior and middle tibiae are almost smooth, even the posterior bristles being minute, but the hind tibia in this species has a very dense band of appressed, stout, bristly setae, both dorsally and ventrally. Moreover, this species has a mat of dense, appressed scales on all of the femora, minutely on the anterior foretibia, but large and conspicuous on the hind tibia. Claws sharp, strongly bent at the middle with large, oval pulvilli.

Wings: Wings large and elongate, sometimes quite broad at the base with a very wide extensive alula and wide axillary lobe or with the wings strongly narrowed toward the base with narrow lobe and alula. In the matter of patterns there are 4 main types of wings in the species: (1) The apical part of the wing is hyaline and the base, to a varying extent, is marked off by uniform, unbroken black, as in the *gideon* Fabricius group. In this group sometimes the entire wing is blackish with only the middles of the cells dilutely paler (*aterrimus* Bigot). (2) The wing is hyaline, except for a few small spots around the basal crossveins and the fucation of the third vein. (3) A comparatively uncommon group in which the wing is entirely hyaline or covered with a uniform tinge of pale brownish yellow. (4) The spots of the wing are very numerous, extending to the apex and posterior border, and with larger areas blocked out in black. Such is the *irrorata* Say group.

The venation within the genus *Anthrax* Scopoli, sensu lato, presents several distinct types. There are those species with 3 submarginal cells formed as in *mystaceum* Macquart, which is the generic type of the genus *Spogostylum* Macquart, and those that have 3 submarginal cells differently formed as in *ocyale* Wiedemann. Another group has only 2 submarginal cells and no trace of spur veins arising either from the second or third veins as in *Anthrax virgo* Egger and *Anthrax aethiops* Fabricius. There is a third group with a constantly present, well-developed spur vein extending backward at the origin of the second vein, which in this case is always rectangular and not rounded as in *stictica* Klug, and which, furthermore, has a strong spur vein at the base of the anterior branch of the third vein. The anal cell is narrowly open or closed in the margin of the wing. The ambient vein is complete, and there is a small basal comb on the costa, which is quite narrow in some species, strongly developed in others. Finally,

the aberrant condition of *Anthrax tigrina* De Geer should be noticed in which the outer bend of the anterior branch of the third vein is sharply rectangular with a short spur and also the curious fifth posterior cell is cut off near the base of the discal cell. Possibly *tigrina* should be placed in a separate subgenus.

Abdomen: Abdomen always short and robust, wider than the thorax, generally rather opaque black, sometimes feebly shining. There are 7 tergites visible from above in both sexes. The pile consists of fine, stiff, erect, bristly hairs of varying length, often arranged in distinct bands, concentrated on the posterior part of the tergites and with the lateral margins having more extensive and more dense, bushy, tufted mats of pile, sometimes of contrasting colors, and sometimes with white or black scales intermixed. These scales may extend over much of the posterior border of the tergites but are apt to be concentrated laterally and there may even be a few scales on the posterior margin of the mesonotum and scutellum. In one group of species the abdomen is covered with a mat of appressed, soft, curled or slightly flattened pile; in another group all the setae are appressed instead of erect; also a rather characteristic group has the whole apex of the abdomen, the last 2 or 3 tergites, covered completely by a dense mat of broad silver scales in the males. Female terminalia largely recessed and hidden by a dense mass of matted curly pile. Male genitalia large in many species. Usually the dististyli are turned straight downward symmetrically side by side. They are quite long, which together with ventral elements make a conspicuous cone-shaped hypopygium.

Inasmuch as Dr. A. J. Hesse has been able to dissect more species than I have, I quote his remarks on the male genitalia:

Hypopygium of males with the two symmetrical clasper-like basal parts always produced basally into a flattened process, their apical part in most cases also produced into a blade-like or prong-like process; beaked apical joints very variable in form and shape, usually much flattened and twisted, or leaf-like, their upper and lower margins extended to a variable extent and the pointed apex or beak usually recurved outwardly and backwardly to a variable extent, sometimes bifid apically or with more than one projection or tooth, their surfaces or upper basal part rarely with conspicuous hairs; aedeagal complex usually with the apical part of the guidepart, which lodges the aedeagus proper, produced ventralwards into a recurved hook or plate, flanked basally on each side by a subsidiary process or tooth, sometimes also with another smaller process on each side, sometimes with a medial flattened key-like or wattle-like extension or even a disc-like expansion below apical part; lateral struts and medial basal strut usually large and well developed, broad, the former usually tongue-shaped, ladle-shaped or shoehorn-shaped, the latter with its dorsal and basal edge often extended on each side into a flange or wing-like extension, its posterior margin sometimes also with a flattened lateral extension. Last sternite opposite hypopygium sometimes slightly notched or indented apically, rarely with its posterior angles produced hook-like. Terminal lamellae in last sternite variable in shape, their dorsapical part produced into a hook-like or spine-like process in some species.

The male terminalia from dorsal aspect, epandrium removed, show a peculiar figure extremely broad on the

basal half, much narrowed on the apical half. The dististyli are small, curious structures, which emit dorsally a hornlike process, curved forward and bluntly pointed. The epiphallus is constricted in the middle and extends beyond the dististylus as a flattened, tongue-like process. From the lateral aspect three things are apparent: the basistylus is club-shaped, strongly expanded at the base, much narrowed apically. Also, there is a long backward triangular lobe from the base, the epiphallus and the ejaculatory processes are both very long, slender, and quite separated. Basal apodeme large and extended backward. The epandrium is curious. It is quite long, apt to be very bristly, almost equally blunt basally as well as apically, with prominent cerci apically, and with a downwardly directed lobe at the base reminiscent of Comptosini, to which of course it bears no relation.

Material available for study: The series of species in the National Museum of Natural History, British Museum (Natural History), Museum of Comparative Zoology, and extensive material in my own collection from the United States, South America, Europe, and Australia.

Immature stages: Immature stages are known for a number of species that parasitize wasps that build mud nests. Also, one species parasitizes a tiger beetle, *Cicindela* species. See under life histories section.

Ecology and behavior of adults: The adults in this genus spend very little time feeding and a great deal of activity given to searching for the nests of their hosts. These flies display much curiosity concerning people, often hovering about the neck or arms of people and alighting on them.

Distribution: Nearctic: *Anthrax albofasciatus* Macquart, 1840 [= *analis* Macquart, 1834], *albofasciatus cascadiensis* Marston, 1963, *albofasciatus piceus* Marston, 1963; *albosparvus* (Bigot), 1892 (as *Argyromoeba*); *analis* Say, 1823; *antecedens* Walker, 1852; *argentatus* (Cole), 1919 (as *Spogostylum*); *argyropygus* Wiedemann, 1828 [= *contigua* (Loew), 1869 (as *Argyromoeba*)]; *aterrimus* (Bigot), 1892 (as *Argyromoeba*); [= *slossonae* (Johnson), 1913 (as *Spogostylum*)]; *aureosquamosus* Marston, 1963, *aureosquamosus chaparralus* Marston, 1963; *cedens* Walker, 1852; *cintalapa* Cole, 1957; *cybele* (Coquillett), 1894 (as *Argyromoeba*); *daphne* (Osten Sacken), 1886 (as *Argyromoeba*); *delila* (Loew), 1869 (as *Argyromoeba*); *fur* (Osten Sacken), 1877 (as *Argyromoeba*); *georgicus* Macquart, 1834; *grossbecki* (Johnson), 1913 (as *Spogostylum*); *irroratus* Say, 1823; *latelimatus* (Bigot), 1892 (as *Hemipenthes*); *limatulus* Say, 1829 [= *obsoleta* (Loew), 1869 (as *Argyromoeba*)], *limatulus artemesia* Marston, 1963, *limatulus colombiensis* Marston, 1963, *limatulus larrea* Marston, 1963, *limatulus vallicola* Marston, 1963; *melanopogon* (Bigot), 1892 (as *Argyromoeba*); *nidicola* Cole, 1952; *occidentalis* (Johnson), 1913 (as *Spogostylum*); *pauper* (Loew), 1869 (as *Argyromoeba*); *plesius* Curran, 1927; *phuricellus* Williston, 1901 [= *capucina* Fabricius of Rau, 1940]; *pluto* Wiedemann,

1828; *seriepunctatus* (Osten Sacken), 1886 (as *Argyromoeba*); *stellans* (Loew), 1869 (as *Argyromoeba*); *tigrinus* (De Geer), 1776 (as *Nemotelus*) [= *scriptus* (Say), 1823 (as *Anthrax*), = *simson* (Fabricius), 1805 (as *Anthrax*)]; *varicolor* (Bigot), 1892 (as *Argyromoeba*); *vierecki* Cresson, 1919 (as *Spogostylum*).

Neotropical: *Anthrax acroleucus* Wiedemann, 1828 [= *gideon* Macquart, not Fabricius, 1840]; *angustipennis* Macquart, 1840; *calopterus* (Schiner), 1868 (as *Argyromoeba*); *cephus* Fabricius, 1805; *crinitus* (Bigot), 1892 (as *Argyromoeba*); *dimidiatus* Wiedemann, 1819; *euplanes* (Loew), 1869 (as *Argyromoeba*); *gideon* Fabricius, 1805; *guianicus* Curran, 1934; *imitans* Schiner, 1868; *inappendiculatus* Bigot, 1892, subg. *Spogostylum*; *leucocephala* Wulp, 1882; *luctuosus* Macquart, 1840; *macquarti* d'Andretta and Carrera, 1952, n.n. [= *leucopyga* Macquart, 1855, not 1840]; *mexicanus* Cole, 1957; *minimaculatus* Oldroyd, 1938; *mystaceus* Macquart, 1840, subg. *Spogostylum*; *oedipus* Fabricius, 1805 [= *aequa* Walker, 1852, = *irrorata* Macquart, 1840, = *punctum* Walker, 1849]; *plurinotus* Bigot, 1892; *pocilophorus* Schiner, 1868; *propinquus* Schiner, 1868; *selenae* Osten Sacken, 1886 [= *obtusius* Coquillett, 1887]; *seriepunctatus* Osten Sacken, 1886, also Nearctic; *squalidus* Philippi, 1865; *subandinus* Philippi, 1865.

Palaeartic: *Anthrax acroleucus* (Bigot), 1892 (as *Argyromoeba*); *actuosus* Paramonov, 1936; *aegypticola* Paramonov, 1936; *aethiops* (Fabricius), 1781 (as *Bibio* and as *Leucamoeba*) [= *punctata* Meigen, 1820]; *aethiops bezzii* Paramonov, 1957; *alagozeicus* Paramonov, 1936; *alashanicus* (Paramonov), 1957 (as *Spogostylum*); *algirus* (Villeneuve), 1910 (as *Argyromoeba*); *anthrax* (Schrank), 1781 (as *Musca*) [= *morio* (Linné), 1758 (as *Musca*), = *sinuata* Meigen, 1804]; *antiopa* (Bezzi), 1924 (as *Spogostylum*); *appendiculatus* Macquart, 1855; *arenivagus* Austen, 1937 (as *Spogostylum*); *aerophilus* Paramonov, 1936; *armeniacus* Paramonov, 1936; *bezzianus* Paramonov, 1936; *binotatus* Wiedemann, 1820 [= *subnotata* Wiedemann, in Meigen, in part, 1820]; *bisniphias* Bezzi, 1925; *boninensis* (Matsumura), 1916 (as *Argyromoeba*); *brevis* Becker, 1913; *brunnicosus* (Becker), 1913 (as *Argyromoeba*); *bucharensis* (Paramonov), 1936; *Paramonovella*, n.n., for *bucharensis* Paramonov, 1957, not 1936; *bucharensis* Paramonov, 1957 (as *Spogostylum*); *cairensis* Paramonov, 1936; *candidus* (Sack), 1909 (as *Psamatamoeba*); *candidapex* Austen, 1937; *caucasicus* (Zaitsev), 1961 (as *Spogostylum*); *chionanthrax* (Bezzi), 1926 (as *Argyromoeba*); *chionostigma* Tsacas, 1962; *chivaensis* Paramonov, 1936; *cineurus* (Zaitsev), 1961 (as *Spogostylum*); *comatus* Austen, 1937 (as *Spogostylum*); *comptus* Paramonov, 1936; *croci* (Villeneuve), 1910 (as *Argyromoeba*); *desertorum* Paramonov, 1936; *distigma* Wiedemann, 1828 [= *tripunctata* Wulp, 1868]; *doctus* (Paramonov), 1957 (as *Spogostylum*); *dubius* (Zaitsev), 1961 (as *Spogostylum*); *efflatouni* Paramonov, 1936; *sergeiae*, n.n., for *efflatouni* Paramonov, 1957, not 1936; *efflatouni* (Paramonov), 1957 (as *Spogostylum*); *erythrogaster* Paramonov, 1936;

etruscus (Fabricius), 1794 (as *Satyramoeba*) [= *formosa* Dufour, 1852, = *hetrusca* Fabricius, of authors, = *rubiginipennis* Macquart, 1840, = *satyrus* (Rossi), 1790, not Fabricius (as *Bibio*)]; *flavus* (Sack), 1929 (as *Leucamoeba*); *flavescens* (Sack), 1909 (as *Spogostylum*); *flavipennis* (Sack), 1909 (as *Spogostylum*); *flavipes* Roeder, 1896 (as *Spogostylum*); *griseescens* Paramonov, 1936; *hassani* Paramonov, 1936; *helenae* (Paramonov), 1957 (as *Spogostylum*); *heteropyga* (Sack), 1909 (as *Argyromoeba*); *hippolyta* (Wiedemann), 1828 (as *Spogostylum*) [= *dedecor* (Hermann), 1907 (as *Argyromoeba*), = *villosa* Klug, 1832]; *incitus* Paramonov, 1936; *indigenus* (Becker), 1913 (as *Argyromoeba*); *irroratus* (Klug), 1832 (as *Spogostylum*); *isis* (Meigen), 1820 (as *Psamatamoeba*) [= *binotata*, Wiedemann in Meigen, 1820, = *ixion* Megerle in litt. in Meigen, = *subnotata* Walker, 1871]; *jazykovi* Paramonov, 1936; *jezoensis* Matsumura, 1916; *karavaievi* Paramonov, 1924, subg. *Spogostylum*; *kiritschenkoi* Paramonov, 1936; *koshunensis* Matsumura, 1916; *kozlovi* (Paramonov), 1957 (as *Spogostylum*); *laetus* Paramonov, 1936; *laevipennis* Paramonov, 1936; *lucidus* (Becker), 1902 (as *Argyromoeba*); *macrocerus* Paramonov, 1936; *maculosus* (Sack), 1909 (as *Argyromoeba*); *massimissa* Wiedemann, 1828; *melanistus* (Bezzi), 1925 (as *Argyromoeba*); *mendax* Austin, 1937; *monacha* (Sack), 1909 (as *Chalcamoeba*); *mongolicus* Paramonov, 1936; *montanus* (Paramonov), 1957 (as *Spogostylum*); *monticola* (Paramonov), 1957 (as *Spogostylum*); *nanellus* Paramonov, 1936; *nanus* Paramonov, 1936; *nigrus* Austen, 1937 (as *Spogostylum*); *niphias* (Hermann), 1907 (as *Psamatamoeba*), *niphias bilineatus* Engel, 1934; *nitidus* Austen, 1937 (as *Spogostylum*); *obuchovae* (Paramonov), 1957 (as *Spogostylum*); *ocybalus* (Wiedemann), 1828 (as *Anthrax*), (subg. *Spogostylum*); *ogasaravensis* Matsumura, 1916; *oophagus* Paramonov, 1936; *oophagus parvus* Paramonov, 1936; *obscurus* (Sack), 1909 (as *Anthraxmoeba*); *pallipes* (Loew), 1869 (as *Spogostylum*); *pamirensis* (Paramonov), 1957 (as *Spogostylum*); *pargriseus* Paramonov, 1936; *Paramonovella*, n.n., for *bucharensis* Paramonov, 1957; *parobscurus* (Paramonov), 1957 (as *Spogostylum*); *perfectus* Becker, 1923; *perpusillus* Austen, 1937 (as *Spogostylum*); *persicus* Paramonov, 1936; *pharaonis* Paramonov, 1936; *pilosulus* Strobl, 1902; *pilosulus tadjikorum* Paramonov, 1936; *punctipennis* (Zaitsev), 1961 (as *Spogostylum*); *putealis* Matsumura, 1905; *ramsesi*, Paramonov, 1936; *repetekianus* Paramonov, 1936; *rufulus* (Zaitsev), 1961 (as *Spogostylum*); *sacki* Paramonov, 1936; *sergeiae*, n.n., for *efflatouni* Paramonov, 1957; *semirufus* Sack, 1909 [= *semifura* Sack, lapsus, 1909]; *shelkovnikovi* Paramonov, 1936; *sordidus* Sack, 1909, subg. *Spogostylum* [= *antiopa* Bezzi, 1925]; *stackelbergi* (Paramonov), 1957 (as *Spogostylum*); *stepensis* Paramonov, 1936; *stricticus* Klug, 1832 [= *polystigma* Sack, 1909]; *submacrocerus* Paramonov, 1936; *tenebrosus* (Paramonov), 1957 (as *Spogostylum*); *transcaspius* Paramonov, 1936; *trifasciatus* Meigen, 1804 [= *aethiops*

Laboulbene (not Fabricius), 1873, [= *capitalata* Mul-sant, 1952], *trifasciatus leucogaster* Wiedemann in Meigen, 1820; *trinotatus* Dufour, 1852, [= *trinaculata* Becker, 1908, Sack, 1909, Engel, 1936], *trinotatus areolatus* Abren, 1926; *tripunctatus* (Wiedemann in Meigen), 1820 (as *Molybdamoeba*) [= *difficilis* Wiedemann in Meigen, 1820]; *turanicus* Paramonov, 1936; *turcomenicus* Paramonov, 1926; *turkmenicola* (Paramonov), 1957 (as *Spongostylum*); *turkmenorum* Paramonov, 1936; *ultrareolatus* Abren, 1926; *uralensis* Paramonov, 1936; *varius* Fabricius, 1794; *velox* Loew, 1862; *virgo* (Egger), 1859 (as *Chalcamoeba*), *virgo pedemontanus* Griffin, 1896, *virgo pilosulus* Strobl, 1902; *volitans* Wiedemann, 1828; *vulpinus* (Sack), 1909 (as *Chrysamoeba*); *yamashiroensis* Matsumura, 1916; *zonabripagus* Portschinsky, 1895; *fulvipes* Loew.

Ethiopian: *Anthrax aethiocomia* (Hesse), 1956 (as *Argyramoeba*); *aygulus* Fabricius, 1805 [= *biflexus* Loew, 1852]; *badius* Hesse, 1956; *bifarius* Hesse, 1956; *bunionicus* François, 1960; *caffer* Hesse, 1956; *camptocladus* Bezzi, 1912; *candidulus* Hesse, 1956; *chalcivorus* Hesse, 1956; *consobrinus* Hesse, 1956, *consobrinus suffusipunctis* Hesse, 1956; *cunctorum* Hesse, 1956; *cuthbertsoni* Hesse, 1956; *dagomba* (Bowden), 1964 (as *Argyramoeba*); *decipiens* (Bezzi), 1912 (as *Molybdamoeba*); *diffusus* Wiedemann, 1824 [= *maculipennis* Macquart, 1840], *diffusus decussus* Bezzi, 1924, *diffusus fuscopurpuratus* Hesse, 1956, *diffusus hybridus* Hesse, 1956, *diffusus majuscus* Bezzi, 1924, *diffusus pallidulus* Hesse, 1956, *diffusus suffusipennis* Hesse, 1956; *dimidiatipennis* Hesse, 1956; *doliops* Hesse, 1956, *doliops fulviventris* Hesse, 1956, *doliops ganka* Hesse, 1956; *dolomatus* Bowden, 1964; *dubius* Macquart, 1840; *elutus* Bezzi, 1921; *erenobius* Hesse, 1956; *eurypterus* Hesse, 1956; *fracidus* (Bowden), 1964 (as *Argyramoeba*); *fratercula* (Bowden), 1964 (as *Argyramoeba*); *fulvastra* (Bowden), 1964 (as *Argyramoeba*) [= *ventrale* (Bezzi), 1924 (as *Spongostylum*)] *fulvipes* Loew, 1860; *furvus* Hesse, 1956; *fuscipennis* Ricardo in Forbes, 1903 [= *dentata* (Becker), 1906 (as *Argyramoeba*), = *muscaria* Klug, 1832]; *hessii* Wiedemann, 1828; *homogeneous* Bezzi, 1912; *immaculatus* (Bowden), 1964 (as *Argyramoeba*); *incisuralis* Macquart, 1840, *incisuralis aridicola* (Hesse), 1956 (as *Argyromoebe*), *incisuralis fumosus* (Hesse), 1956 (as *Argyromoebe*), *incisuralis glaucescens* (Hesse), 1956 (as *Argyromoebe*), *intermedius* Hesse, 1936; *kaokoensis* Hesse, 1956; *laminelus* Speiser, 1910; *leucopogon* (Bezzi), 1912 (as *Molybdamoeba*); *leucurus* Hesse, 1956, *massauensis* Jaennicke, 1867; *mimetes* Hesse, 1956; *mixtus* Loew, 1860; *munroi* Hesse, 1956, *munroi willowmorensis* Hesse, 1956; *muticus* Bezzi, 1921 (as *Spogostylum*); *namaensis* Hesse, 1956; *nanus* Hesse, 1956; *nigerrimus* Bezzi, 1924, *nigerrimus ocellatus* Bezzi, 1924; *nubeculosus* Hesse, 1956; *phaeopteralis* Hesse, 1956; *pithecius* Fabricius, 1805 [= *confusumaculata* Macquart, 1855, = *conspurcata* Wiedemann, 1828, = *spectabilis* Loew, 1860]; *plumipes* Hesse, 1956; *princeps* Bezzi, 1924; *punctipennis* Wiedemann, 1821; *puncturellus* Hesse, 1950; *punicisetosus* (Hesse), 1955 (as *Argyro-*

moeba); *pycnopeltis* (Hesse), 1956 (as *Argyromoebe*); *quinquemaculatus* Bezzi, 1924 (as *Spogostylum*); *rhodesiensis* Hesse, 1956; *robustalis* (Hesse), 1956 (as *Argyromoebe*); *saturatus* Bezzi, 1924 (as *Spogostylum*); *simmillimus* Hesse, 1956; *spathistylus* Hesse, 1956; *sticticalis* Hesse, 1956; *subanthrax* Bezzi, 1924; *tetraspilus* Hesse, 1956; *triatomus* Hesse, 1956 [= *trimaculatus* Bezzi, not Wulp, 1921]; *triguttellus* Hesse, 1956; *trisinuatus* Hesse, 1956; *trixus* Bowden, 1964; *xerous* Hesse, 1956.

Oriental: *Anthrax appendiculatus* (Bigot), 1892 (as *Argyromoebe*); *argentiapicalis* (Brunetti), 1912 (as *Argyromoebe*); *austeni* Brunetti, 1920; *bipunctatus* Fabricius, 1805; *carbo* Rondani, 1875; *ceylonicus* Brunetti, 1909, *claripennis* Brunetti, 1909; *clausus* Brunetti, 1909; *distigma* Wiedemann, 1828 [= *argyropyga* Dole-schall, 1857, = *tripunctata* Wulp, 1868]; *duvaucellii* Macquart, 1840; *fallax* de Meijere, 1907; *fletcheri* Brunetti, 1920; *fulvulus* Wiedemann, 1821 [= *degener* Walker, 1856, = unnamed variety Wulp, 1880]; *gentilis* Brunetti, 1909; *gestroi* Brunetti, 1912; *guttatipennis* Brunetti, 1920; *himalayensis* Brunetti, 1909; *indicatus* Nurse, 1922; *intermedius* Brunetti, 1920; *limitarsis* Brunetti, 1909; *leucopygus* Macquart, 1840; *melania* Wulp, 1885; *nigrofemoratus* Brunetti, 1909; *niveicauda* Brunetti, 1920; *niveisquamis* Brunetti, 1909; *obscurifrons* Brunetti, 1909; *semiscitus* Walker, 1857.

Australian: *Anthrax arcus* de Meijere, 1913; *ater* Roberts, 1928; *confluens* Roberts, 1928; *lepidiota* Roberts, 1928; *proconceus* Hardy [= *conceus* Macquart, 1849, not Macquart, 1840]; *prosimplex* Hardy [= *simplex* Macquart, 1847]; *velox* White, 1917.

Ignota Patria: *Anthrax degenera* Walker, 1852a.

Genus *Dicranoclista* Bezzi

FIGURES 160, 403, 679, 753, 1018, 1019, 1020

Dicranoclista Bezzi, The Bombyliidae of the Ethiopian Region, p. 178, 1924. Type of genus: *Dicranoclista simpsoni* Bezzi, 1924, original designation.

Coquillettia Williston, Manual North American Dipt., Ed. II, p. 65, 1896b. Type of genus: *Spogostylum vandykei* Coquillett, 1894, by original designation. Preoccupied by Uhler, 1890.

Shining black flies, with dense, erect, rather long, plushlike, reddish yellow to yellowish-brown pile upon thorax and abdomen and easily recognized by the peculiar venation of the wing. The vein that is the anterior branch of the third vein coalesces and is confluent for quite a distance with the posterior branch of the second vein, but this branch of the third vein rejoins the last branch of the third vein so that there is an extra submarginal cell corresponding to the fourth cell in *Ligyra* Newman. Moreover, the attachment of the second branch of the second vein is atrophied and directed back ward as a spur from the point of coalescence so that there is in fact only 3 submarginal cells. First posterior cell is also closed and stalked. The second vein arises

quite rectangularly and has a strong backward spur. The wing is quite hyaline on the outer half, the base being wholly brown to yellow or subhyaline with the veins narrowly brown and a vertical spot of brown of varying size on the anterior crossvein and extending up to the wing margin.

Antennae typical of the Anthracinae; the third segment is very short and broad, the style slender, with 2 segments and a pencil of hairs at the apex. Pile of front fine and erect, of face coarse and erect, short beneath antennae, long and mustache-like above the oral margin; appressed scales lie along the middle of the front. Squama and alula with fine pile, the former dense and bushy. Anterior tibia long and slender with numerous, fine, long spines.

Three species are known, one from Gambia, one from Utah, and a third species, *vandykei* Coquillett, from California, Utah, and Texas. Johnson and Johnson (1960) note that the latter species peculiarly resembles *Chrysanthrax fulvianus* Say in general appearance.

Length: 10 to 12 mm.; wing: 9 mm.

The antennae are attached a little below the middle of the head. The first segment is widened apically, is only a little longer than the second, and bears a few, fine hairs of no great length laterally and dorsolaterally and some shorter ones medially. The second segment is shorter than wide, fully and broadly attached to the base of the third segment. The third segment is quite short and onion-shaped with a short, stylar, asymmetrical portion directed laterally, slightly knobbed apically, and bearing a short microsegment with apical brush or circle of hairs.

Head, lateral aspect: Head subglobular, the occiput is very prominent and extensive dorsally, even more so in the middle of the eye at the point of indentation, but ventrally the occiput is only about half as long as it is dorsally. Pile of the occiput consists of narrow, flat-appressed, scattered scales, more dense at the point of indentation, but also with a tuft of erect hair at this point. Interior cup of the occiput large and deep with a dense fringe of short pile on the border. The front is convex, quite extensive, scarcely raised above the eye margin, but with numerous scattered, appressed, long, slender scales and with abundant, coarse erect pile extending from the ocellar tubercle nearly to the antenna. The scales overlap the base of the antenna. From the lateral aspect, very little of the face shows. It retreats downward slightly below the eye margin, the total depth of the face is almost equal the length of the antenna. There is a conspicuous, circular, transverse band of dense, coarse, almost bristly, reddish pile, reaching from the eye margin across the lower face. The eye is reniform with a deep, wide excavation, the upper and lower angles are approximately equal, and there is a bisecting line at the midpoint of the eye. Upper facets of the eye in the male very slightly enlarged. The proboscis is short and stout and confined to the oral recess and the labellar portion comprises at least four-fifths

of its length. The palpus is quite short, small, and clavate with a few stiff hairs near the apex.

Head, anterior aspect: The head is not quite as wide as the thorax. The eyes are rather widely separated in the male by 3 times the width of the ocellar tubercle. Their width also a little more than the width of the antennae. The ocellar tubercle is quite small but prominent and the ocelli occupy an equilateral triangle. Antennae widely separated, the space between equals the space between antenna and eye. Below the face the eyes are slightly convergent with deep, sloping sides almost reaching to the bottom of the oral recess. Oral recess narrowed a little before the middle, the posterior part quite deep with vertical walls. Gena very narrow. Tentorial pits deep. From above, the lobes of the occiput are tightly apposed, with a comparatively deep fissure.

Thorax: The thorax is considerably longer than wide. The mesonotum and the scutellum are shining black with very dense, reddish-yellow, plushlike pile which in nowise obscures the ground color, and this pile becomes even more dense broadly along the anterior margin and on the humerus. There are 3 or 4 distinct bristles on the notopleuron. The pile on the propleuron, mesopleuron, and pteropleuron is quite dense. The hypopleuron and metapleuron are bare, but there is a tuft of long pile posteriorly behind the spiracle. The metanotum appears to be exceptionally short and appears to be bare. The squama has a fringe of dense, matlike hair. The plumula has a wide band of long pile.

Legs: The legs are stout, all of the femora being strengthened without being swollen. The first four femora are, however, a little wider basally. First four femora also with a fringe of hairs distally. Hind femur with a ventrolateral row of 12 to 15 oblique, sharp, slender bristles and at least 10 bristles ventromedially besides scattered appressed setae dorsally on at least the outer half. All of the femora are densely covered with very broad, loosely appressed, large, brownish-yellow scales. Anterior tibia slender, elongate with some 16 slender prominent though short spiculate bristles anterodorsally and 20 bristles posterodorsally. There are 12 or 14 similar bristles posteroventrally. Middle tibia similar with an additional true ventral row containing few bristles. Hind tibia with 6 or 7 bristles anteroventrally and 10 to 12 bristles in each dorsal row. Claws large, long, sharp, strongly bent at the apex, the pulvilli quite long and spatulate.

Wings: Hyaline in the type-species with the basal third completely brownish yellow filling the anal cell, axillary lobe and alula, filling the second basal cell and extending beyond as a triangle into the discal and fourth posterior cell, and extending upward to the first vein and moreover filling almost all of the costal cell and with a broad spot covering the anterior crossvein and reaching up to the first vein. In the American species *vandykei* Coquillett the wing is in every respect similar to the type-species, except that the brownish-yellow color is found only at the base of the wing,

borders the posterior margin of the second and anterior border of the third basal cells, fills out the whole of the costal and subcostal cells, and has only a small spot on the anterior crossvein and base of second vein. In *fasciata* Johnson and Johnson the dark color of the wing is almost restricted to the prehumeral area of the wing and to the costal cell. This genus is very unique in the presence of an extra submarginal cell formed much as in *Ligyra* Newman, except that there is an addition and incomplete spur constantly present extending back toward the second vein. As I interpret this wing the anterior branch of the third vein and posterior branch of the second vein coalesced at some time in the past to present this formation. The first posterior cell is closed and stalked. There is a well-developed basal comb and a stout basal hook. Ambient vein complete. *Alula* large.

Abdomen: Abdomen oval, narrowed somewhat posteriorly. Bezzi (1924) says of the type-species that the abdomen is a little pointed. It is a little wider basally than the thorax, rather flattened, shining black with dense, erect pile of considerable length, somewhat more loose and sparse medially, but certainly very dense laterally and upon the lateral margins. The ground color is in no way obscured and there are no bristles. In the American species the posterior margins of the second, fifth, and sixth tergites have a complete band of conspicuous, leaf-shaped, brownish-yellow scales; curiously these scales on the third and fourth tergites are restricted to a short row on the lateral margin. Male genitalia symmetrical, pale in color. The dististyle is directed downward.

Material available for study: The type-species in the British Museum (Natural History) and also material of *vandykei* Coquillett.

Immature stages: Unknown.

Ecology and behavior of adults: I have seen no record of adult behavior, except that Johnson and Johnson (1960) record taking a female of *fasciata* Johnson and Johnson on a twig before sunrise by the Provo River, Utah.

Distribution: Nearctic: *Dicranoclista fasciata* Johnson and Johnson, 1960; *vandykei* (Coquillett, 1894 (as *Spogostylum*)).

Ethiopian: *Dicranoclista simpsoni* Bezzi, 1924.

Genus *Walkeromyia* Paramonov

FIGURES 164, 165, 411, 426, 677, 709, 730, 746, 748, 750, 751

Walkeromyia Paramonov, Konowia, vol. 13, p. 23, 1934c. Type of genus: *Anthrax luridus* Walker, 1857, by original designation.

Large, robust, brownish, or brownish-yellow, or reddish-black, shining flies, which have a strongly swollen front and face, much reduced fleshy proboscis and labellum, and correspondingly shortened, ventral oral recess. Related most closely to Anthracinae with which it agrees in the type of mouth, wing venation and espe-

cially in the bare metapleuron in front of the haltere, and in the simple pile of the squama. It is aberrant in that the long, conical, third antennal segment has a minute, short style without any hair tuft at the apex. A further peculiarity lies in the fact that the hind legs of the male have dorsally and ventrally a long dense band of slender black scales extending from basal third of the femur to include the first 3 segments of the tarsus. Wing generally uniformly brownish yellow; 2 submarginal cells; anterior branch of third vein arising plane, not quite at right angles but with long backward spur.

Two species, from southern part of South America and from Trinidad.

Length: 14 to 19 mm.; wing 16 to 21 mm., the wing longer than the body.

Head, lateral aspect: Head almost globular, with the occiput exceptionally produced and strongly projected backward. The length of the occiput at the vertex is even greater than the width of the male vertex, and even greater in extent if measured from the deep indentation of the posterior eye margin. The occiput is slightly more extensive in males than in females, and, viewed from above, shows 3 or 4 faint transverse grooves. Instead of being produced directly backward, the occiput slopes posteriorly almost as much as the eye slopes anteriorly. The central indentation on the posterior eye margin is very broad and deep, the angle above equal to the angle below; posterior part of eye with bisecting line. Pile of occiput scanty, short, appressed and setate, and forming longer tufts of stiff hair in the hollow of the indentation, these bristly hairs directed forward. The fringe about the deep occipital cup is scanty below, dense above.

The front is very large and extensive, a little swollen, and at the level of the antennae, almost twice as wide as the width at the vertex. The pile of the front consists of scattered, fine, erect hairs of no great length, but with 6 patches of similar denser hair, 3 distributed on the upper part of the front and 3 distributed across the front on its lower third. The face is quite extensive, swollen like the front, rounded and convex, produced forward, its length equal the conical part of the third antennal section, pile of face comparatively dense, coarse, black and bristly, its length slightly greater than the pile of the front. There is a distinct bare space beneath each antenna. Oral recess small and deep, confined to the lower eighth of the head. It is deep and the posterior part in which the proboscis is imbedded has vertical walls. This swollen ridgelike genal sidewall, almost as wide as the oral recess, curves abruptly inward anteriorly so as to form a deep, transverse recess and extension of the posterior part and has on each side a deep tentorial pocket. The proboscis is shorter than in *Anthrax* Scopoli and fully two-thirds of the proboscis is composed of the swollen clublike labellum. Palpus clavate with minute setae and as long as the basal part of the proboscis. Antennae attached at the middle of the head, widely separated, the first and second segments

are both quite short, the first segment is twice as long as the second, the third segment is a little wider than the second, closely attached to it, short conical with a narrow stylar portion not more than one-fifth the total length of the segment. Attached to the apex of the third segment is a very small, thick, short, pale, bristle-tipped microsegment. There is no circlet of hairs at the apex of the segments.

Head, anterior aspect: The head is slightly flattened above, below and on each side, and it is slightly wider below. The vertex in males and females is of almost equal width and is about three-fourths as wide as the genal space between the eyes below. The antennae are widely separated, each attached at the outer third of the face. Ocellar tubercle low, the ocelli placed in a short isosceles triangle, oral opening deep and short rectangular, widening laterally in front; the genae are pollinose and without pile. Viewed from above, the occiput has a deep, long fissure, the sides touching, the cleft deeply recessed.

Thorax: The thorax is a little longer than wide, widest posteriorly, and wider than the head. It is feebly shining, very dark brown in color. The pile is fine, erect, and rather short in the middle of the mesonotum, but there is a considerable amount of curled, appressed pile laterally and posteriorly and the anterior collar pile is considerably longer and erect. Bristles are absent. Scutellar pile appressed and consisting of narrow scales. Upper mesopleuron with a dense tuft of pile, the anterior half appressed forward, the posterior half appressed backward. Pteropleuron with quite abundant pile. The hypopleuron and the metapleuron in front of the baltere are bare. Metanotum beneath the scutellum very short and apparently bare. Squama with a short fringe of hair.

Legs: Weak on the anterior forelegs. The hind legs, however, are quite long and strongly developed although slender. In the male there is a curious, dense, wide, rather dense band of brownish black, long, slender scales, which begin a little before the middle of the hind femur and form a dorsal and ventral feathered band on the hind femur, both dorsal and ventral surfaces of the hind tibia, and both surfaces of first two segments of the hind tarsus. The band of scales on the hind femur is broadest below, but on the tibia and tarsus it is much more extensive dorsally than below. Hind basitarsus more than twice as long as the remaining segments. Claws and pulvilli well developed.

Wings: The wings are quite large and long, extending far beyond the apex of the abdomen, uniformly tinged with brownish-yellow color. There are 2 submarginal cells and a backward spur vein arises near the base of the anterior branch of the third vein. The second arises rectangularly, and the anterior crossvein is placed at the middle of the discal cell. There is a short spur vein backward from the medial crossvein below the discal cell. Anal vein narrowed apically and also narrowly open. Alula comparatively narrow. The ambient vein is complete. There is a small basal comb on

the costa; also a distinct, flattened, apically rounded lobe.

Abdomen: Abdomen robust, shorter than the thorax in males, of about equal length in females. It is strongly convex across the middle. I find 6 tergites visible in the male, 7 in the female. The abdomen is rather densely covered with matted, slender, appressed, shining black scales, and a few wider scales laterally and along the posterior edges of the tergites and also laterally some stiff, bristly hair which tends to become more conspicuous and often matted into tufts along the posterior border of the last tergite and the last sternite. Male terminalia deeply recessed and enclosed by bands of stiff long black hair. Female terminalia similarly concealed.

Material available for study: A pair of *turidus* Walker lent by the National Museum of Natural History and additional material purchased from Fritz Plaumann.

Immature stages: The host and larval forms have not been recorded, as far as I am aware, but in the National Museum of Natural History there is a female from Trinidad that was reared in a nest of *Xylocopa submordax* by F. D. Bennett, who deserves much credit for having preserved this record.

Ecology and behavior of adults: Not on record. Probably very similar to *Anthrax tigrinus* Fabricius, which also parasitizes bees of the genus *Xylocopa* Latreille. I believe these anthracine flies should fall within a separate tribe, the Walkeromyini. This requires that *Anthrax tigrinus* Fabricius be placed within a genus separate from other North American *Anthrax* Scopoli. I propose *Stymphalina*, new name.

Distribution: Neotropical: *Walkeromyia lurida* Walker, 1857; *plumipes* Philippi, 1873.

Genus *Coniomastix* Enderlein

FIGURE 412

Coniomastix Enderlein, Deutsche Ent. Zeitschr., 1934, p. 140, 1934. Type of genus: *Coniomastix montana* Enderlein, 1933, by original designation.

I have not seen *Coniomastix* Enderlein and I quote his description.

Genus of the subfamily Anthracinae. Eyes somewhat indented or excavated (posteriorly). Antenna flagellum (microsegment) extraordinarily short and in the form of a minute cone; it bears on the point scattered little hairs. In front of the ocelli, there is a sharply impressed frontal furrow or indentation reaching as far as the ocellar tubercle. The second and third branches of the radius at the base with vein stumps. Base of radius two and radius three (appearing as a crossvein) and also a spur situated proximal before the radiomedial crossvein. Fourth longitudinal vein strongly bent forward towards the front; the second and third branches bent more weakly. The fifth band of radius and first of medius end separately, likewise the second cubitus and the two middle branches of the medius. The crossvein between the second radius and the third and fourth is complete.

Distribution: Palaearctic: *Coniomastix montana* Enderlein, 1933.

Supplemental Text Figures

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THE HISTOGENESIS AND EVOLUTION OF INTEGUMENTS IN ONAGRACEAE¹

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ABSTRACT

The mode of initiation and subsequent growth of the inner (i.i.) and outer (o.i.) integuments were examined and compared in 40 species, representing all seven tribes and all 17 genera of Onagraceae. The i.i. is of dermal origin and two-layered throughout the family. Four different types of developmental mode of the o.i. are characterized: 1) o.i. of subdermal origin—*Lopezia* (Lopezieae), *Fuchsia* (Fuchsieae), and *Circaea* (Circaeae); 2) o.i. of both dermal and subdermal origin, with derivatives of the subdermal cells dividing more actively than those of the dermal cells—*Oenothera* and *Stenosiphon* (Onagreae); 3) o.i. of both dermal and subdermal origin, with derivatives of the subdermal cells dividing less actively than those of the dermal cells—*Hauya* (Hauyeae) and *Calylophus* and *Gaura* (Onagreae); 4) o.i. of dermal origin—*Ludwigia* (Jussiaeae), *Boisduvalia* and *Epilobium* (Epilobieae); and *Camissonia*, *Clarkia*, *Gayophytum*, *Gongylocarpus*, *Heterogaura*, and *Xylonagra* (Onagreae). Except for the unexpected close similarity of *Hauya* (Hauyeae) to *Calylophus* and *Gaura* (Onagreae), among which is shared an apparently derived state of this character rather suggesting a common ancestry, the patterns of relationships suggested on the basis of the developmental mode of the o.i. closely accord with those derived from other lines of evidence. The results from Onagraceae confirm that the histogenetic characters of integuments are valuable indicators of relationship at a generic level.

The family Onagraceae, composed of seven tribes, 17 genera, and about 674 species (Raven, 1979), is one of the most intensively investigated families of angiosperms. In recent years, in addition to systematic studies (e.g., Raven, 1963, 1964, 1969; Plitmann et al., 1973), there have also been studies on chromosome number and morphology (e.g., Kurabayashi et al., 1962; Raven & Gregory, 1972; Raven & Tai, 1979), wood anatomy (Carlquist, 1975, 1977, 1982), pollen morphology (e.g., Skvarla et al., 1975, 1978), floral anatomy (Eyde & Morgan, 1973; Eyde, 1977, 1978, 1981, 1982), and leaf anatomy (Keating, 1982). As a result of these detailed

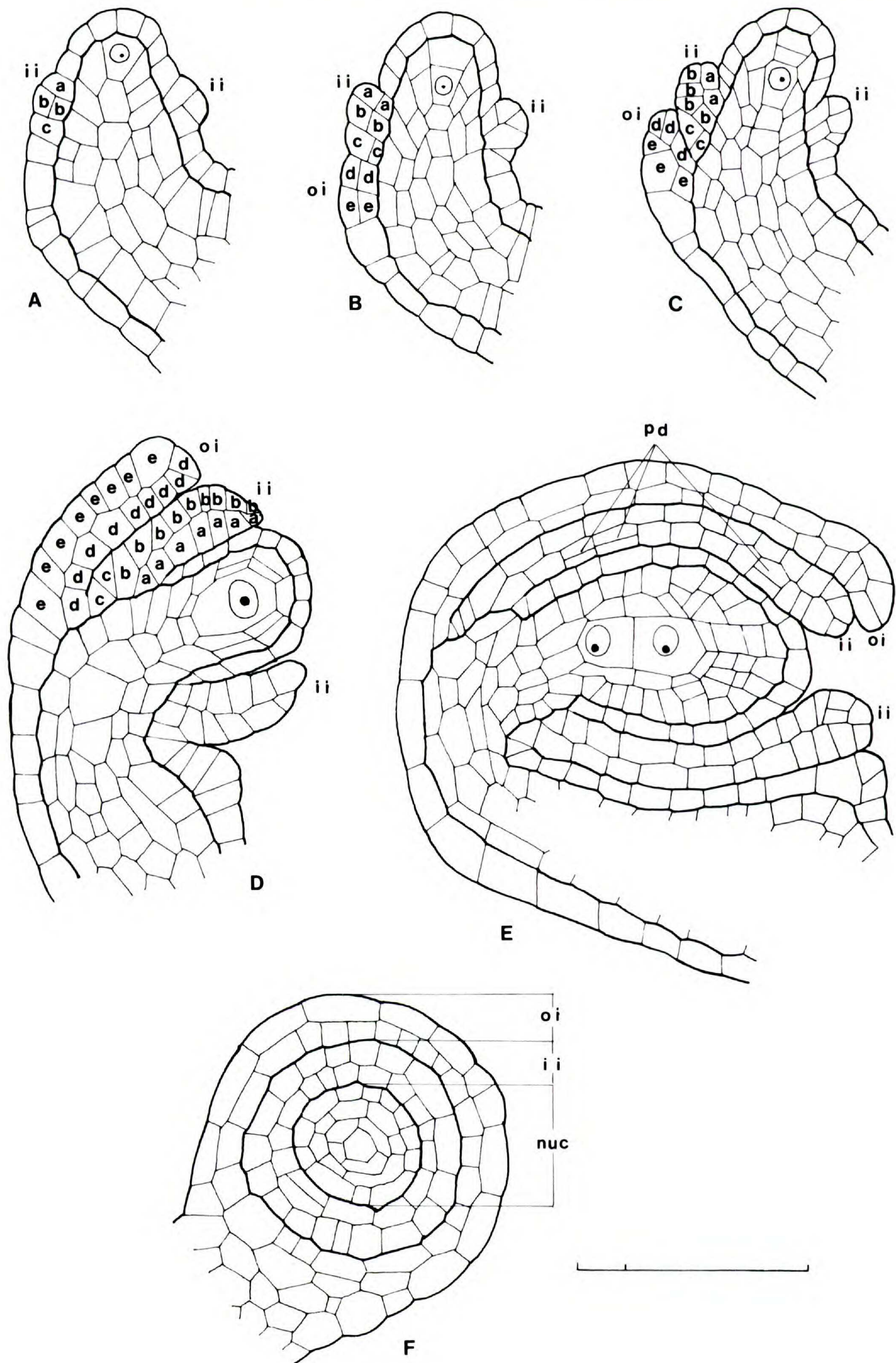
studies, our knowledge of phylogenetic relationships within the family at a generic level has become quite detailed.

The major outlines of the pattern of relationships that have been revealed are as follows. *Ludwigia* represents a line distinct from all other genera of the family (Eyde, 1977, 1978, 1981; Raven & Tai, 1979). It shares with two of the more primitive genera in the other phylogenetic branch of the family, namely *Fuchsia* (Fuchsieae) and *Hauya* (Hauyeae), the generalized characteristic of lacking interxylary phloem (Carlquist, 1975, 1977). In addition to *Fuchsia* and *Hauya*, *Lopezia* (Lopezieae) and *Circaea* (Circaeae), in

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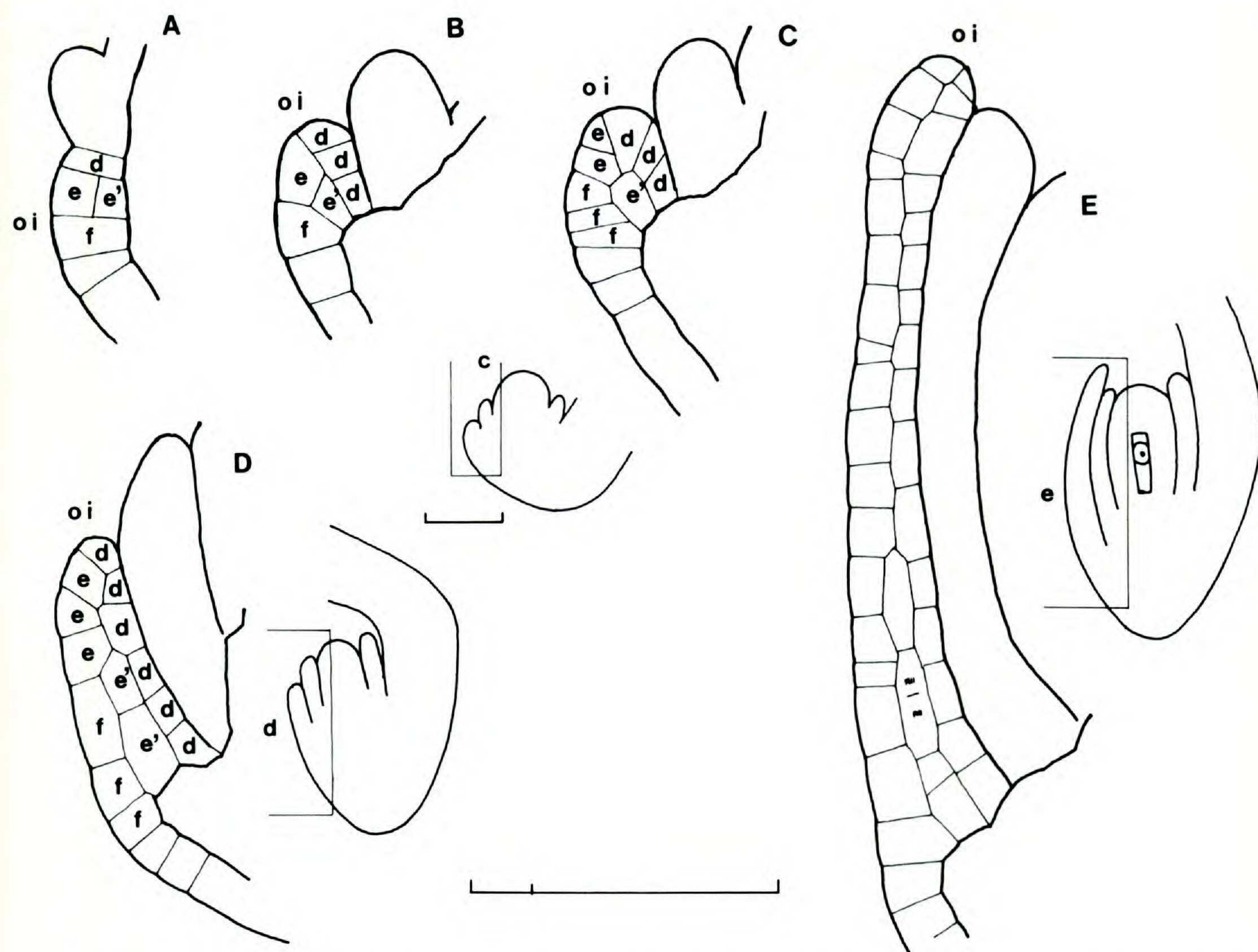


FIGURE 2. *Ludwigia peploides*.—A–E. Median longisections of the o.i. in progressively successive stages of development, showing the development of a distinctive three-layered part of the o.i. d, e, f, dermal initials of the o.i.; e', daughter cell of the dermal initial e, and functioning as an initial for the third (middle) layer of the o.i. Bracket scales = 100 μ m.

which at least the most primitive species have a basic chromosome number of $n = 11$, present an array of relatively primitive characteristics, so that *Circaea*, *Fuchsia*, *Hauya*, and *Lopezia* may be regarded as distantly related, generalized lines within this major branch of the family—the branch that does *not* include *Ludwigia*. Epilobieae, consisting of *Boisduvalia* and *Epilobium* only, is advanced in many of its characteristics but occupies a rather isolated position within the family (Raven, 1976). Within the group of ten genera recognized as Onagreae (Raven, 1964,

1969), *Clarkia* and *Heterogaura* constitute one distinctive group; *Oenothera* and *Stenosiphon* another; *Calylophus* and *Gaura* a third; and *Camissonia*, *Gongylocarpus*, *Gayophytum*, and *Xylonagra* a fourth (Tobe & Raven, 1985). *Hauya* (Hauyeae) has been separated as a distinct tribe by virtue of its generalized characteristics including the presence of stipules, generalized leaf anatomy distinct from that of all Onagreae (Keating, 1982), and lack of interxylary phloem. On the other hand, its possession of obviously divided sporogenous tissue generally similar to

FIGURE 1. *Ludwigia arcuata*.—A–D. Median longisections of ovule primordia in progressively successive stages of development, showing that both the inner (i.i.) and outer (o.i.) integuments are of dermal origin. a, b, c, dermal initials of the i.i.; d, e, dermal initials of the o.i.—E. Median longisection of a growing ovule, in which periclinal cell divisions (pd) take place in the inner layer of the i.i.—F. Cross section of a growing ovule. nuc, nucellus. Bracket scale = 100 μ m.

TABLE 1. A comparison of histogenetic characteristics of integuments in Onagraceae. Degree of participation of derivatives of subdermal initials in formation of the outer integument (o.i.) defined as follows: (+ + +) up to the tip of o.i. (see Fig. 10A); (+ +) more than half as much as, but less than, the whole length of o.i. (see Fig. 10B); (+) up to only the basal part of o.i. (see Fig. 10C); (–) no derivatives of subdermal initials contribute to the formation of o.i. (see Fig. 10D).

Taxon	Locality and Collection Information	Number of Cell Layers in Integument		Origin of Outer Integument	Degree of Participation of Derivatives of Subdermal Initials in Formation of Outer Integument
		Inner	Outer		
Tribe Jussiaeae					
<i>Ludwigia arcuata</i> Walt.	U.S.A. Florida: Hillsborough Co., Peng 4320 (MO).	2	2	dermal	–
<i>L. bonariensis</i> (Michx.) Hara	Argentina. Buenos Aires: La Plata, Ramamoorthy 1005 (MO).	2	2	dermal	–
<i>L. peploides</i> (H.B.K.) Raven	U.S.A. Missouri: St. Louis Co., Tobe, 1981 (MO).	2	2–3	dermal	–
<i>L. lanceolata</i> Ell.	U.S.A. Georgia: McIntosh Co., Peng 4139 (MO).	2	2	dermal	–
<i>L. linearis</i> Walt.	U.S.A. Louisiana: St. Tammany Parish, Dille 420 (MO).	2	2	dermal	–
<i>L. leptocarpa</i> (Nutt.) Hara	Brazil. Bentos: Santa Catarina, Ramamoorthy 1134 (MO).	2	2	dermal	–
<i>L. virgata</i> Michx.	U.S.A. Alabama: Mobile Co., Tobe, 1981 (MO).	2	2	dermal	–
<i>L. peruviana</i> (L.) Hara	Australia. Mascot (7 km S of Sydney), Briggs 7143 (NSW).	2	2	dermal	–
<i>L. latifolia</i> (Benth.) Hara	Costa Rica. Puntarenas, Raven 21575 (MO).	2	2	dermal	–
Tribe Lopezieae					
<i>Lopezia langmaniae</i> Miranda	Mexico. Chiapas, Breedlove 32300 (CAS).	2	3–4	subdermal	+ + +
<i>L. racemosa</i> Cav. subsp. <i>racemosa</i>	Mexico. Chiapas, Breedlove 7030 (CAS).	2	3–4	subdermal	+ + +
<i>L. semeiandra</i> Plitmann, Raven & Breedlove	Mexico. Sinaloa, Breedlove 8044 (CAS).	2	3–4	subdermal	+ + +
Tribe Fuchsiaeae					
<i>Fuchsia radicans</i> Miers.	Brazil. São Paulo: Campas de Jordão, Ramamoorthy 676 (MO).	2	3–6	subdermal	+ + +
<i>F. jimenezii</i> Breedlove, Berry & Raven	Costa Rica. Monteverde Preserve, Haber, Baker & Baker 434 (MO).	2	3–4	subdermal	+ + +

TABLE 1. Continued.

Taxon	Locality and Collection Information	Number of Cell Layers in Integument		Origin of Outer Integument	Degree of Participation of Derivatives of Subdermal Initials in Formation of Outer Integument
		Inner	Outer		
<i>F. microphylla</i> H.B.K. subsp. <i>quercetorum</i> Breedlove	Cultivated, Univ. Calif. Bot. Gard. (Berkeley), <i>Raven</i> , 1969 (MO).	2	3-6	subdermal	+++
Tribe Circaeae					
<i>Circaea cordata</i> Royle	Cultivated, Missouri Bot. Gard. #762431, original plants collected by Raven in 1975 from Vladivostok, USSR (MO).	2	3-5	subdermal	+++
<i>C. alpina</i> L. subsp. <i>pacifica</i> (Asch. & Mag.) Raven	Cultivated, Univ. British Columbia Bot. Gard. (UBC).	2	3-5	subdermal	+++
Tribe Hauyeae					
<i>Hauya elegans</i> DC. subsp. <i>elegans</i>	Mexico. Chiapas, <i>Breedlove</i> 42631 (MO).	2	2-5	dermal and subdermal	+
<i>H. heydeana</i> Donn. Smith	Mexico. Chiapas: Ocotol Grande, <i>Breedlove</i> 15669 (MO).	2	2-5	dermal and subdermal	+
Tribe Onagreae					
<i>Gongylocarpus fruticosus</i> (Benth.) Raven & Breedlove	Mexico. Baja California: Magdalena Is., <i>Verity</i> 037 (MO).	2	2	dermal	-
<i>G. rubricaulis</i> Schlecht. & Cham.	Mexico. Chiapas, <i>Breedlove</i> 41880 (CAS).	2	2	dermal	-
<i>Gayophytum humile</i> Juss.	U.S.A. Oregon: Jefferson Co., <i>Chambers</i> 4834 (OSC).	2	2	dermal	-
<i>G. heterozygum</i> Lewis & Szwey.	U.S.A. Oregon: Jefferson Co., <i>Chambers</i> 4835 (OSC).	2	2	dermal	-
<i>Xylonagra arborea</i> (Kellogg) Donn. Smith & Rose	Mexico. Baja California, <i>Verity</i> , <i>Nakai & Angel</i> , 1979, no voucher.	2	2	dermal	-
<i>Camissonia ovata</i> (Nutt. ex Torr. & A. Gray) Raven	U.S.A. California: Marin Co., <i>Raven & Raven</i> 26148 (MO).	2	2	dermal	-
<i>C. californica</i> (Nutt. ex Torr. & A. Gray) Raven	Cultivated, UCLA Bot. Gard., <i>Verity</i> , no voucher.	2	2	dermal	-

TABLE 1. Continued.

Taxon	Locality and Collection Information	Number of Cell Layers in Integument		Origin of Outer Integument	Degree of Participation of Derivatives of Subdermal Initials in Formation of Outer Integument
		Inner	Outer		
<i>Calylophus lavandulifolius</i> (Torr. & A. Gray) Raven	U.S.A. Nevada: Lincoln Co., Tiehm & Williams 6572 (MO).	2	2-3	dermal and subdermal	+
<i>C. serrulatus</i> (Nutt.) Raven	U.S.A. Kansas: Sherman Co., Brooks 15533 (KANU).	2	2-3	dermal and subdermal	+
<i>Gaura coccinea</i> Pursh	U.S.A. Texas: Pecos Co., Powell 3589 (MO).	2	2-4	dermal and subdermal	+
<i>G. longiflora</i> Spach	U.S.A. Missouri: Jefferson Co., Wagner, Mill & Tobe 4522 (MO).	2	2-3	dermal and subdermal	+
<i>Oenothera flava</i> (A. Nels.) Garrett subsp. <i>flava</i>	Mexico. Durango, Wagner & Solomon 4321 (MO).	2	2-5	dermal and subdermal	++
<i>O. villosa</i> Thunb. subsp. <i>villosa</i>	U.S.A. Missouri: St. Louis Co., Wagner, Chin & Tobe 4519 (MO).	2	2-5	dermal and subdermal	++
<i>Stenosiphon linifolius</i> (Nutt.) Heynh.	U.S.A. Oklahoma: McClain Co., Sullivan 1038 (OKL).	2	2-4	dermal and subdermal	++
<i>Clarkia delicata</i> (Abrams) Nels. & Macbr.	Mexico. Baja California, Moran 27640 (MO).	2	2	dermal	-
<i>C. tenella</i> (Cav.) Lewis subsp. <i>tenella</i>	Chile. Malleco: Curacao, Marticorena & Ovezada 1669 (MO).	2	2	dermal	-
<i>Heterogaura heterandra</i> (Torr.) Coville	U.S.A. California: Tuolumne Co., Gottlieb, 1977 (MO).	2	2	dermal	-
Tribe Epilobieae					
<i>Boisduvalia subulata</i> (Ruiz. & Pavón) Raimann	Chile. Ñuble, Cheese & Watson 4405 (K).	2	2	dermal	-
<i>B. glabella</i> (Nutt.) Walp.	U.S.A. California: Yolo Co., Crampton 9212 (MO).	2	2	dermal	-
<i>Epilobium ciliatum</i> Raf. subsp. <i>watsonii</i> (Barbey) Hoch & Raven	U.S.A. California: Marin Co., Sharp, 1967 (MO).	2	2	dermal	-
<i>E. canum</i> (Greene) Raven subsp. <i>canum</i>	Cultivated, Univ. Calif. Bot. Gard. (Berkeley) UCBG 58.996 (UC).	2	2	dermal	-

that found in *Calylophus*, *Clarkia*, *Gaura*, and *Heterogaura*, has been used as evidence for linking it with these groups (Raven, 1964, 1969, 1979), as have its vespertine flowers, long floral tubes, white petals, and strong floral odor, this syndrome of characteristics closely resembling that found in white-flowered species of *Oenothera*.

The histogenesis of integuments which is the subject of this paper is used here as another approach to clarify the relationships between the genera of Onagraceae. Although such characteristics have traditionally been included within the scope of investigations of embryologists, they have largely been confined to considerations of the number and thickness of the integuments, the development of integuments into seed coats, and the participation of integuments in formation of the micropyle. In contrast, little attention has been devoted to the developmental mode of the outer and inner integuments (see reviews in Bouman, 1971, 1974, 1984). Twenty-five years ago, the studies of Roth (1957) on *Capsella* began to interest embryologists again in the developmental mode of integuments, a field that had been largely neglected since the studies of Warming (1878) over a century ago. The subsequent works of Bouman and his collaborators on *Juglans* and *Pterocarya* (Boesewinkel & Bouman, 1967), on Polycarpicae (Bouman, 1971, 1977, 1978; Boer & Bouman, 1972, 1974), and on Rutaceae (Boesewinkel, 1977, 1978; Boesewinkel & Bouman, 1978) have increasingly called our attention to the histogenetic characters of integuments as a probable indicator of affinity among taxa. Bouman (1971) emphasized the importance of observations of the histogenesis of integuments in their evaluation, citing the fact that seemingly identical structure of integuments often developed as a result of different histogenetic processes. He also warned against the taxonomic value of data based on the structure of the mature seed coat for similar reasons. For example, *Drimys winteri* Forst. (Winteraceae) has an outer integument of dermal origin (Boer & Bouman, 1974), whereas *Magnolia stellata* (Sieb. & Zucc.) Maxim., *M. virginiana* L., and *Liriodendron tulipifera* L. (Magnoliaceae) have an outer integument of subdermal origin (Boer & Bouman, 1972; Bouman, 1977). This difference in the histogenetic origin of the outer integument has been used as additional evidence for separating Winteraceae from Magnoliaceae, with which they were combined earlier (Boer & Bouman, 1974).

We have made observations of the histogenesis of the integuments as part of a study of the embryology of Onagraceae. In this paper we shall deal only with the mode of initiation and subsequent growth of the integuments, not considering the more diversified morphology of the seed coat or testa. We shall utilize the mode of initiation and subsequent growth of integuments solely as an indicator of affinity between taxa and shall attempt neither morphological interpretations of these structures nor detailed studies of other aspects of embryology in these plants.

Only one earlier paper deals with the histogenesis of integuments of Onagraceae (Geerts, 1908). Geerts provides excellent illustrations of the young ovules of *Oenothera glazioviana* Mich. (= "*O. lamarckiana*"), stating "Das innere Integument entwickelt sich nur aus Dermatogenezellen, zur Bildung des äusseren Integumentes finden im Periblem Teilungen statt." Several other papers dealing with the embryology of Onagraceae (e.g., O'Neal, 1923, *Oenothera biennis* L. = "*O. rubrinervis*"; Johansen, 1934, *Circaea alpina* subsp. *pacifica* = "*C. pacifica*"; Täckholm, 1914, *Lopezia racemosa* subsp. *racemosa* = "*L. coronata*") have illustrations of sections of young ovules including views of developing integuments; all of these papers, however, lack an explanation of the histogenesis of the structures illustrated and are not detailed enough to be used in connection with this present comparative study.

MATERIALS AND METHODS

Forty species representing all seven tribes and all 17 genera of Onagraceae were included in our study. They are listed in Table 1, along with the results obtained from each. All the samples were fixed in FAA (90 parts 50 or 70% ethanol, 5 parts acetic acid and 5 parts formalin) and then dehydrated through tertiary-butyl alcohol series and embedded in paraplast. Serial microtome sections of ovaries 5–7 μ m thick were stained with Heidenhain's hematoxylin, safranin, and fast green FCF.

In all Onagraceae, the ovule has two integuments, inner (i.i.) and outer (o.i.); it becomes anatropous or hemitropous (*Lopezia*) at maturity. The terminology, abbreviation of terms, and the manner of drawing microtome sections basically follow Bouman (1974). In every diagram illustrating the histogenesis of integuments, Figures 1, 2, 4–8 for example, bold lines are used

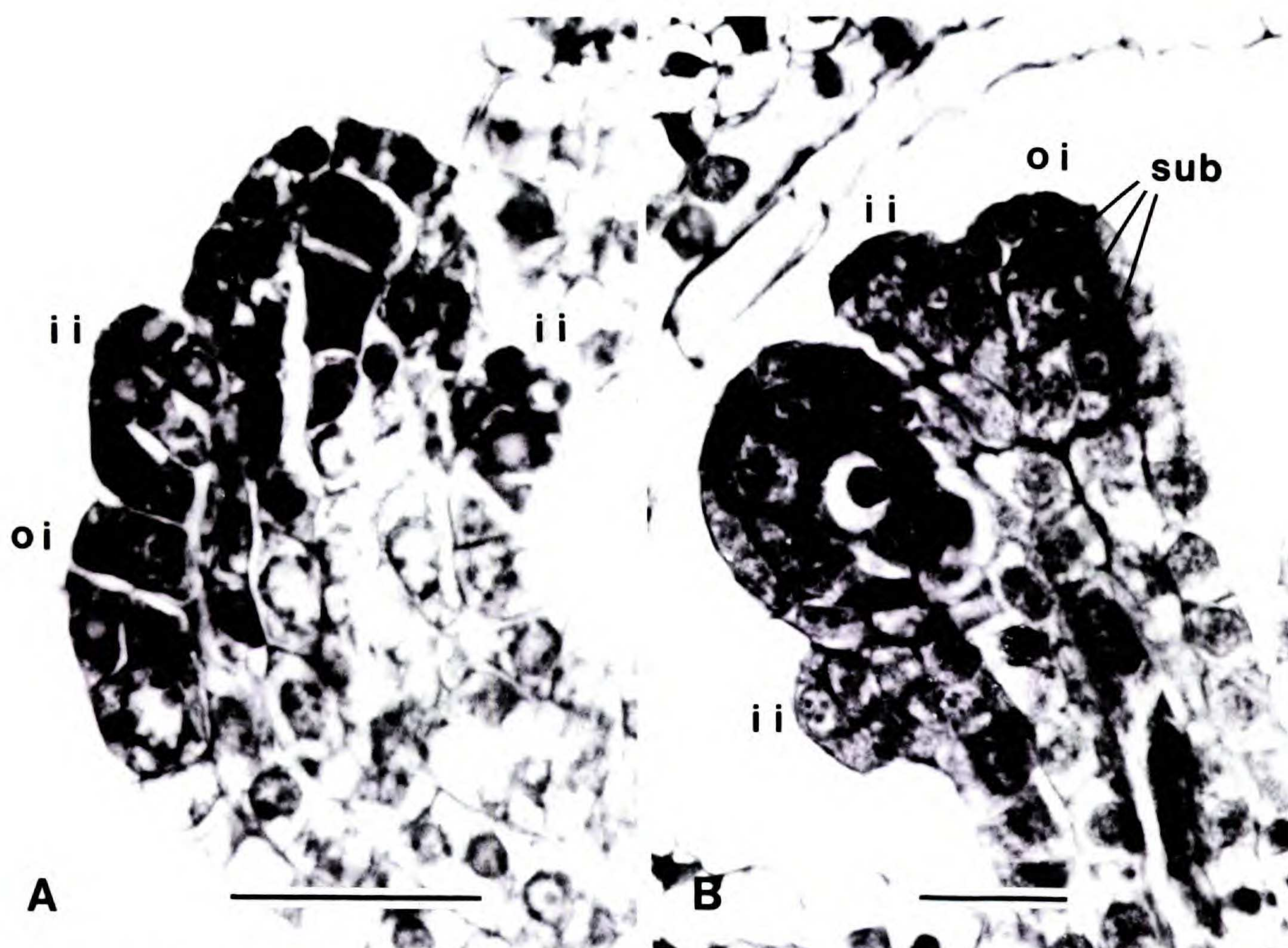


FIGURE 3. Median longisections of the ovule primordia, showing two contrasting developmental modes of the o.i.—A. *Ludwigia arcuata*. Note that the o.i. is initiated dermally.—B. *Lopezia racemosa*. Note that the o.i. is initiated subdermally. Scales = 20 μ m.

to represent the boundary between dermal and subdermal tissues.

OBSERVATIONS

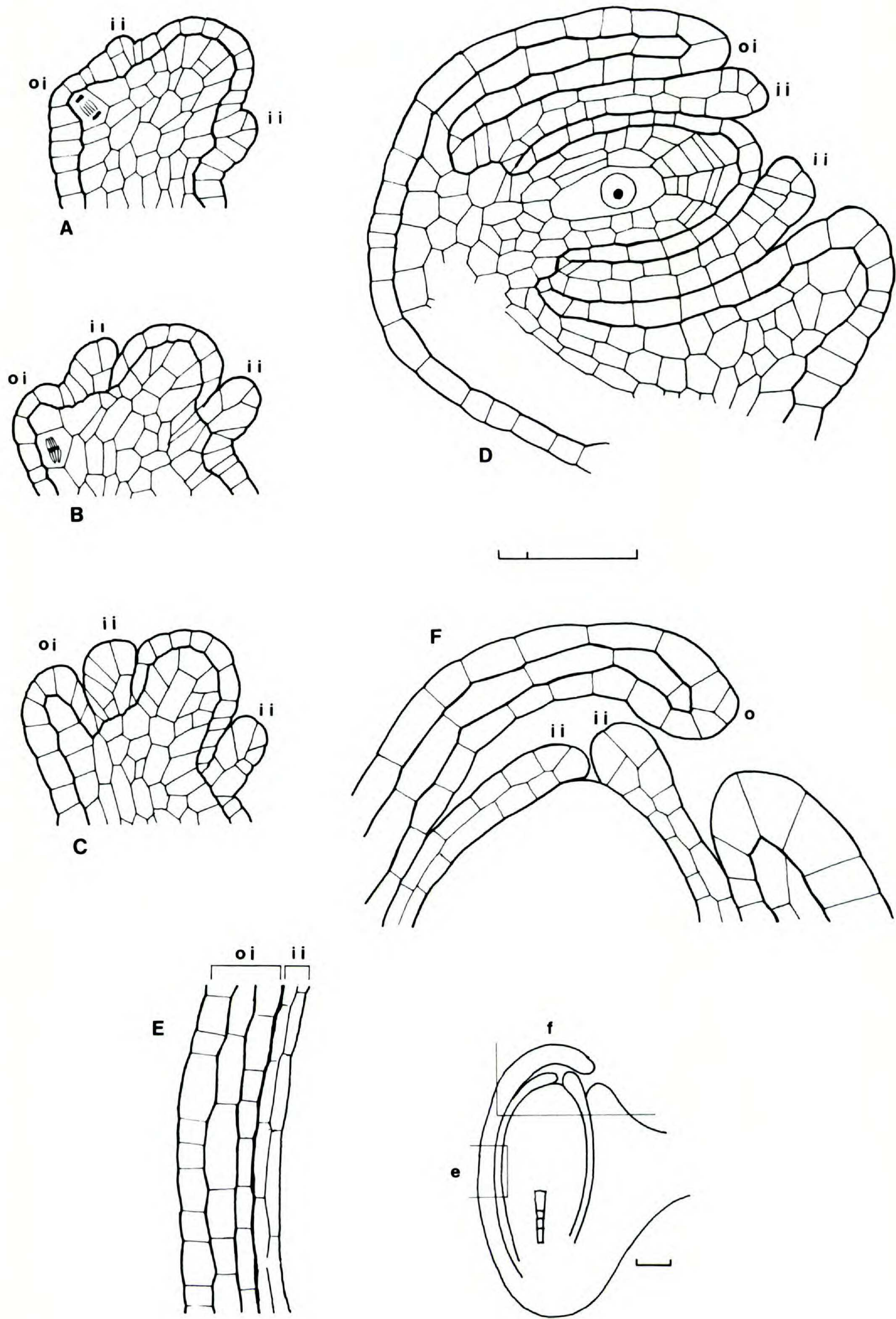
TRIBE JUSSIAEEAE

Ludwigia arcuata, *L. bonariensis*, *L. latifolia*, *L. leptocarpa*, *L. linearis*, *L. peploides*, *L. peruviana*, and *L. virgata*—In every species the initiation of the i.i. commences by periclinal divisions of dermal cells located at the flank of an ovule primordium (Fig. 1A, see cells b). In median longisections of the ovule primordium, three dermal initial cells (a, b, c in Fig. 1B; see also Fig. 3A), or occasionally only two, a and b, were

recognized. The first periclinal divisions of these three initials form a swelling of the i.i., first discernible externally. The subsequent growth of the i.i. primordium takes place chiefly by divisions of daughter cells of two, a and b, initials (Fig. 1C, D), so that the i.i. grows as a two-layered thin organ. In a developed ovule the i.i. usually becomes three-layered because of periclinal divisions of cells of the inner layer of the i.i. (Fig. 1E, F). The tip of the i.i. ultimately becomes multilayered, forming an endostome similar to that known in many other angiosperms.

Thus, since the initiation and the subsequent growth of the i.i. takes place by divisions of dermal initials and their derivatives, the i.i. of *Lud-*

FIGURE 4. *Lopezia semeiandra*.—A–C. Median longisections of ovule primordia in progressively successive stages of development, showing that the i.i. is of dermal origin but the o.i. of subdermal origin.—D. Median longisections of a growing ovule.—E. Longisection of a lateral part of a developed ovule.—F. Longisection of a micropylar part of a developed ovule. Note that the derivatives of the subdermal initials reach up to the tip of the o.i. Bracket scales = 100 μ m.



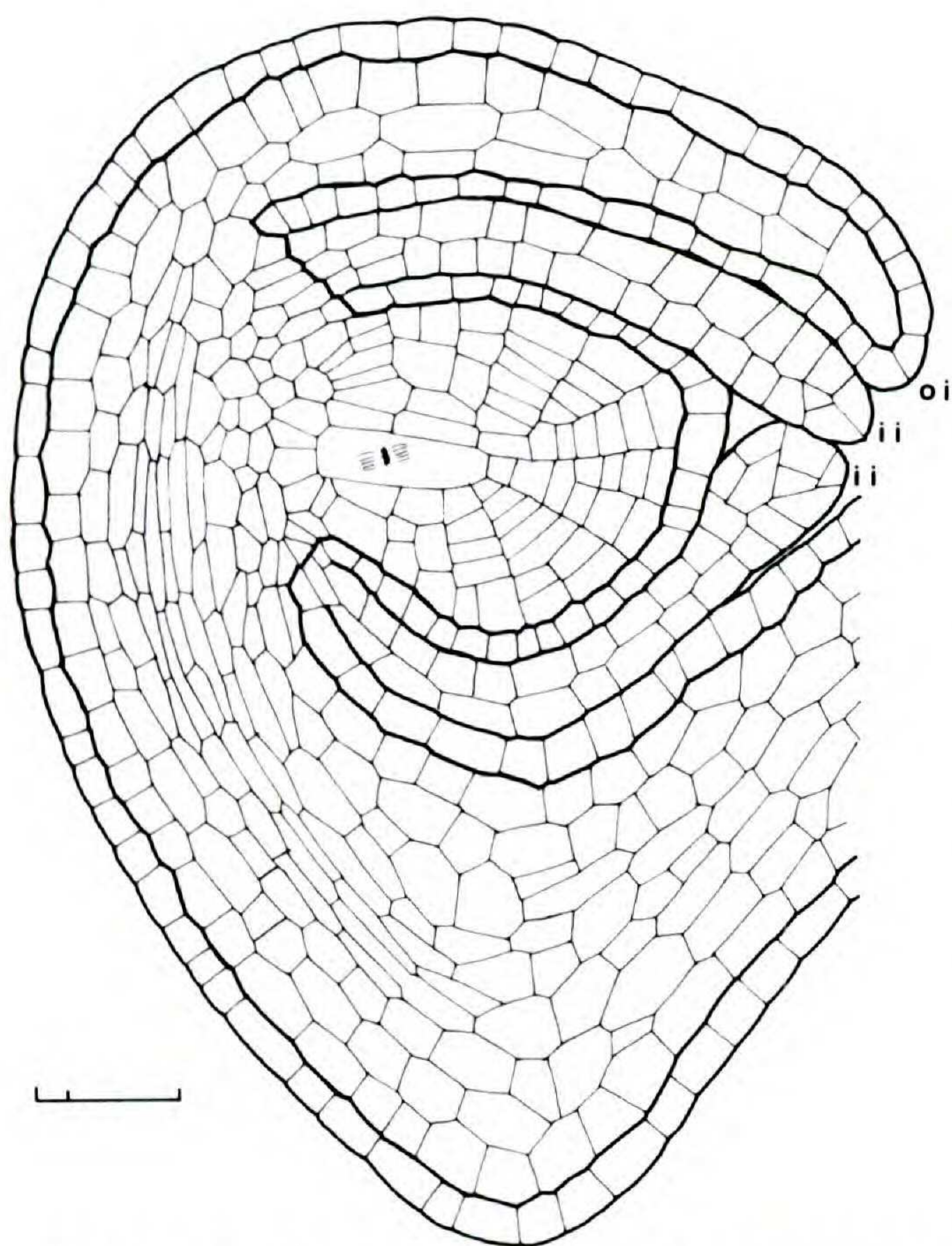


FIGURE 5. *Fuchsia radicans*. Note that the o.i. is of subdermal origin and the derivatives of the subdermal initials reach up to the tip of the o.i. Bracket scale = 100 μ m.

wigia is of dermal origin, a term used consistently by Bouman and his collaborators to express this pattern of development.

The o.i. is also of dermal origin in all species examined. At the initiation stage, two dermal initials (d, e in Fig. 1B; see also Fig. 3A) undergo periclinal divisions. Subsequent growth takes place by repeated divisions of derivatives of the dermal initials (Fig. 1C, D). The mature o.i. is two-layered in all the species except *L. peploides* (Fig. 1E, F), and only its tip becomes multilayered to form an exostome. The o.i. hardly develops at the funicular side, and, if it does, it is made up on this side of derivatives of dermal initials only (Fig. 1E).

In the sole exceptional species, *L. peploides*, a developed o.i. is two-layered in the upper part and three-layered in the lower part (Fig. 2E). This three-layered part of the o.i. is formed in a different mode from that of the i.i. The first periclinal division of the dermal initial e gives rise to two daughter cells, the lower cell e' functioning as a distinct initial of the third (middle) layer in

the subsequent growth (Fig. 2A, B). Consequently, the upper part of the o.i. grows by divisions of the upper daughter cell e as well as of another initial d, and the lower part by divisions of derivatives of an additional initial f as well as of e' and d (Fig. 2C, D).

TRIBE LOPEZIEAE

Lopezia langmaniae, *L. racemosa* and *L. semeiandra*—The i.i. is of dermal origin and two-layered in all species examined (Fig. 4A–F).

The mode of initiation and the subsequent growth of the o.i. is consistent in all species examined, differing completely from the pattern seen in *Ludwigia*. On the antiraphial and lateral sides, the initiation of the o.i. commences by periclinal divisions of subdermal cells, and not by those of dermal cells (Fig. 4A). Repeated periclinal divisions of subdermal cells give rise to a primordium of the o.i. discernible externally as a swelling (Fig. 4B, C; see also Fig. 3B). Subsequent growth proceeds by divisions of both subdermal and dermal cells (Fig. 4D). Thus, even if dermal cells will have divided periclinally to make an exostome at the tip of the o.i., derivatives of the subdermal initials reach the tip on all antiraphial and lateral sides (Fig. 4F). The mature o.i. is usually three-layered in the upper part and three- to four-layered in the lower part (Fig. 4E, F). In *Lopezia*, the mature ovule is hemianatropous, and therefore the o.i. is well developed on the funicular side also (Fig. 4D).

Thus, since subdermal initials and their derivatives contribute to the formation of the integument, the o.i. of *Lopezia* is of subdermal origin, a term used to express a mode contrasting with that in *Ludwigia*.

TRIBE FUCHSIEAE

Fuchsia jimenezii, *F. microphylla* subsp. *quercetorum*, and *F. radicans*—The i.i. is of dermal origin and two-layered in all species examined.

The o.i. is of subdermal origin in all species examined. Derivatives of subdermal initials participate in the formation of a major part of the o.i., and reach its apex as in *Lopezia* (Fig. 5). The thickness of the o.i. differs from species to species: three- to four-layered in *F. jimenezii*, and three- to six-layered in *F. radicans* (Fig. 5) and *F. microphylla*.

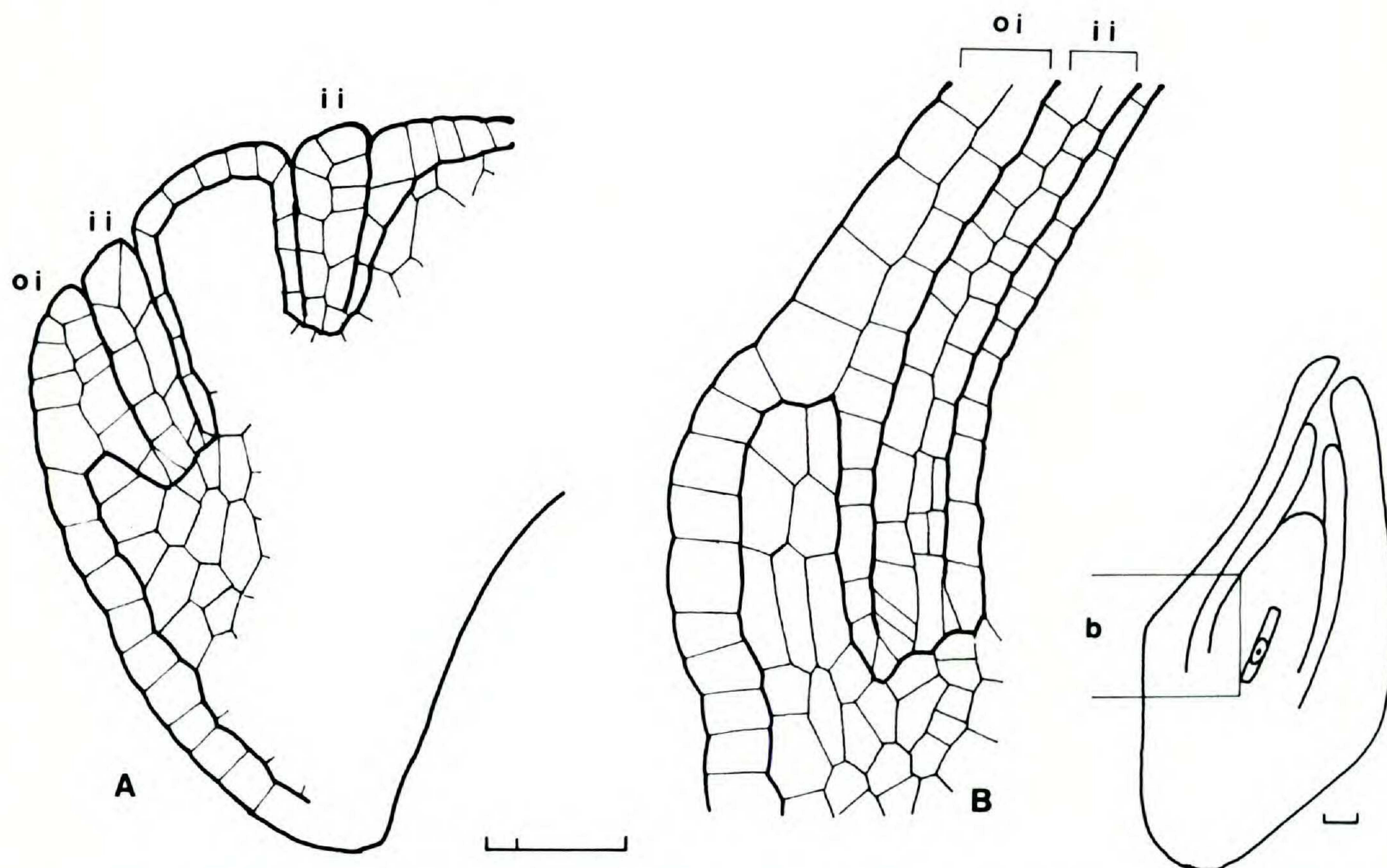


FIGURE 6. *Hauya elegans* subsp. *elegans*.—A. Median longisection of an ovule primordium.—B. Longisection of a developed ovule. Note that the o.i. is of both dermal and subdermal origin, and the derivatives of the dermal initials divide more actively than those of the subdermal ones in the formation of the o.i. Bracket scales = 100 μ m.

TRIBE CIRCAEEAE

Circaea alpina subsp. *pacifica* and *C. cordata*—The i.i. is of dermal origin and two-layered in both species.

The o.i. is of subdermal origin and three- to five-layered in both species. Derivatives of subdermal initials reach the tip of the o.i. as in *Lopezia* and *Fuchsia* (Fig. 9A).

TRIBE HAUYEAE

Hauya elegans subsp. *elegans* and *H. heydeana*—The i.i. is of dermal origin and two-layered in both species (Fig. 6A, B).

The o.i. is of both dermal and subdermal origin in both species. On the antiraphial and lateral surfaces, the initiation of the o.i. commences with periclinal divisions of dermal as well as of subdermal initials (Fig. 6A). Subsequently, however, derivatives of the dermal initials divide more actively than those of the subdermal initials, so that the derivatives of the subdermal initials remain in the basal part of the o.i. on the antiraphial and lateral sides (Fig. 6B). Consequently, the mature o.i. is mostly two-layered, but three-

to five-layered in its basal portion in both species (Fig. 6B).

TRIBE ONAGREAE

Gongylocarpus fruticosus and *G. rubricaulis*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

Gayophytum heterozygum and *G. humile*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

Xylonagra arborea—Both the i.i. and the o.i. are of dermal origin and two-layered.

Camissonia californica and *C. ovata*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

Calylophus lavandulifolius and *C. serrulatus*—The i.i. is of dermal origin and two-layered in both species. The mode of the initiation and the subsequent growth of the o.i. is similar to that in *Hauya*. In both species the o.i. is initiated by periclinal divisions of dermal as well as of subdermal initials (Fig. 7A). Derivatives of the dermal initials divide more often than those of the subdermal initials subsequently (Fig. 7B). Ultimately, the derivatives of subdermal initials par-

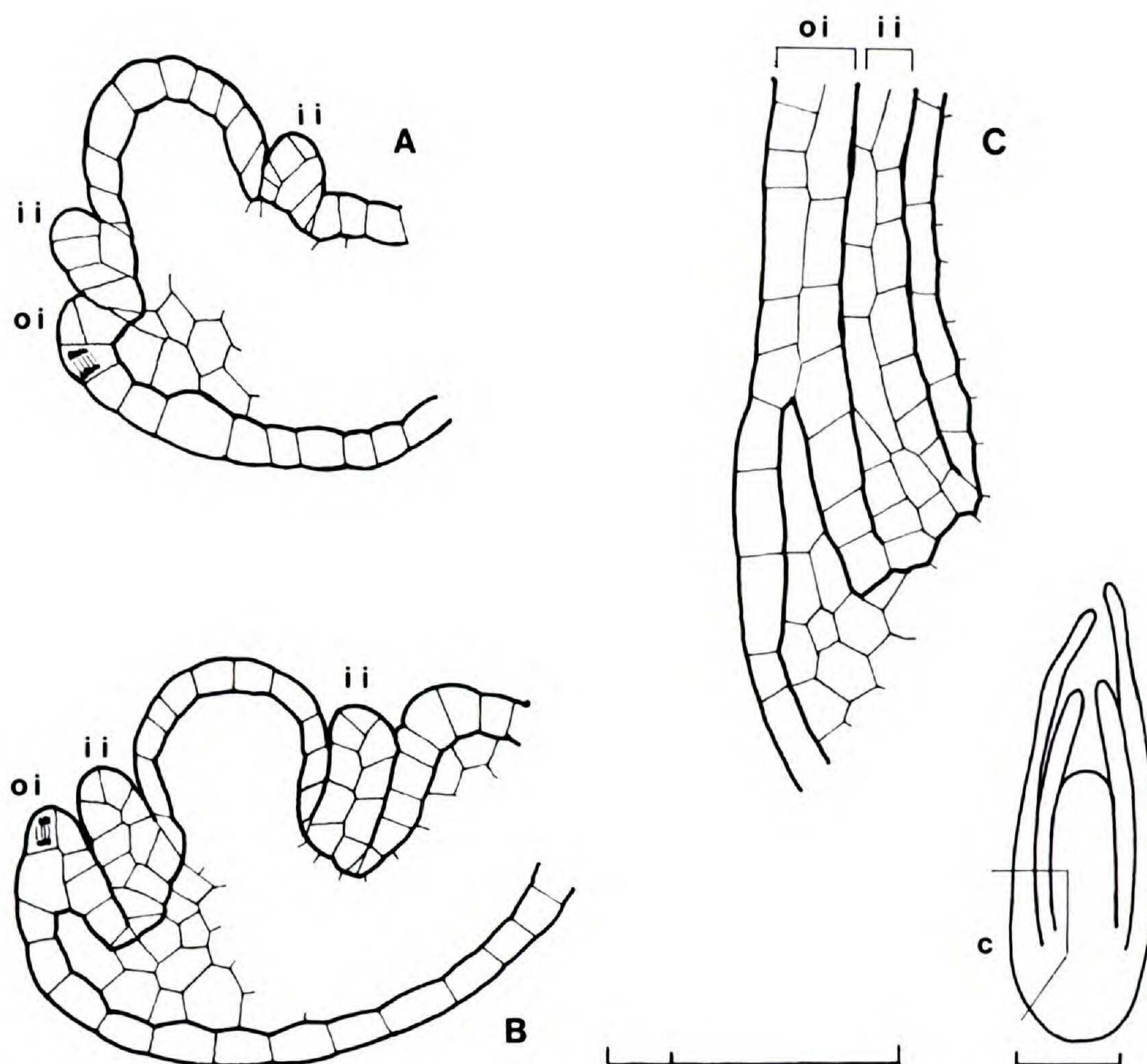


FIGURE 7. *Calylophus lavandulifolius*.—A, B. Median longisections of ovule primordia in progressively successive stages of development, showing that the o.i. is of both dermal and subdermal origin.—C. Longisection of a developed ovule. Note that the derivatives of the dermal initials divide more often than those of the subdermal ones in the formation of the o.i. Bracket scales = 100 μ m.

ticipate only in the formation of the basal part of the o.i. (Fig. 7C). The mature o.i. is mostly two-layered but three- to four-layered in its basal portion (Fig. 7C).

Gaura coccinea and *G. longiflora*—The i.i. is of dermal origin and two-layered, and the o.i. of both dermal and subdermal origin in both species. The degree of participation of derivatives of subdermal initials in the formation of the o.i. closely resembles that seen in *Hauya* and *Calylophus*. Therefore, the mature o.i. is mostly two-layered but three- to four-layered in its basal portion, which is made up of derivatives of dermal and subdermal initials.

Oenothera flava subsp. *flava* and *O. villosa* subsp. *villosa*—The i.i. is of dermal origin, as Geerts (1908) observed, and two-layered in both species. On the antiraphial and lateral sides, the o.i. is of both dermal and subdermal origin in both species. Geerts (1908) mentioned that in *O. glazioviana* (= "*O. lamarckiana*"), the o.i. is produced by divisions of subdermal cells. But his

figure (Geerts, 1908, table 19, fig. 3) illustrating a median longisection of the very young ovule primordium shows the o.i. swelling by divisions of derivatives of both dermal and subdermal initials. In both species examined in this paper, the dermal and the subdermal initials appear to divide almost simultaneously (Fig. 8A). In any event, at least it is obvious that the derivatives of both the dermal and subdermal initials contribute to the formation of the o.i. Of more importance to the final outcome is the fact that the derivatives of the dermal initials divide less actively than those of the subdermal ones, a feature in which *Oenothera* differs from *Hauya*, *Calylophus*, and *Gaura* (Fig. 8B). The mature o.i. is two-layered in the upper portion and three-layered in the lower portion (Fig. 8C).

Stenosiphon linifolius—The i.i. is of dermal origin and two-layered. The mode of initiation and the subsequent growth of the o.i. is almost identical to that in *Oenothera*. On the antiraphial and lateral sides, the o.i. is of both dermal and

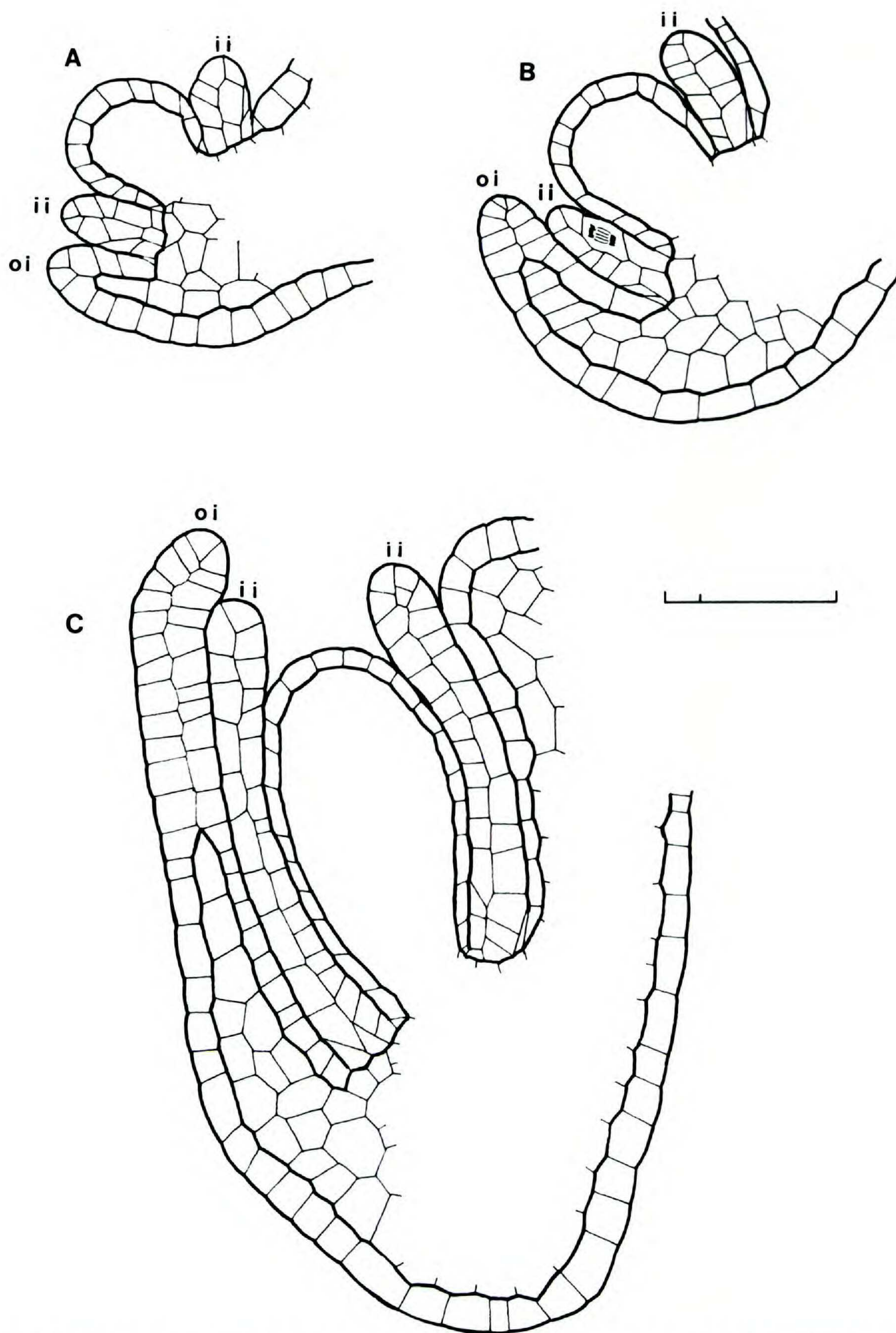
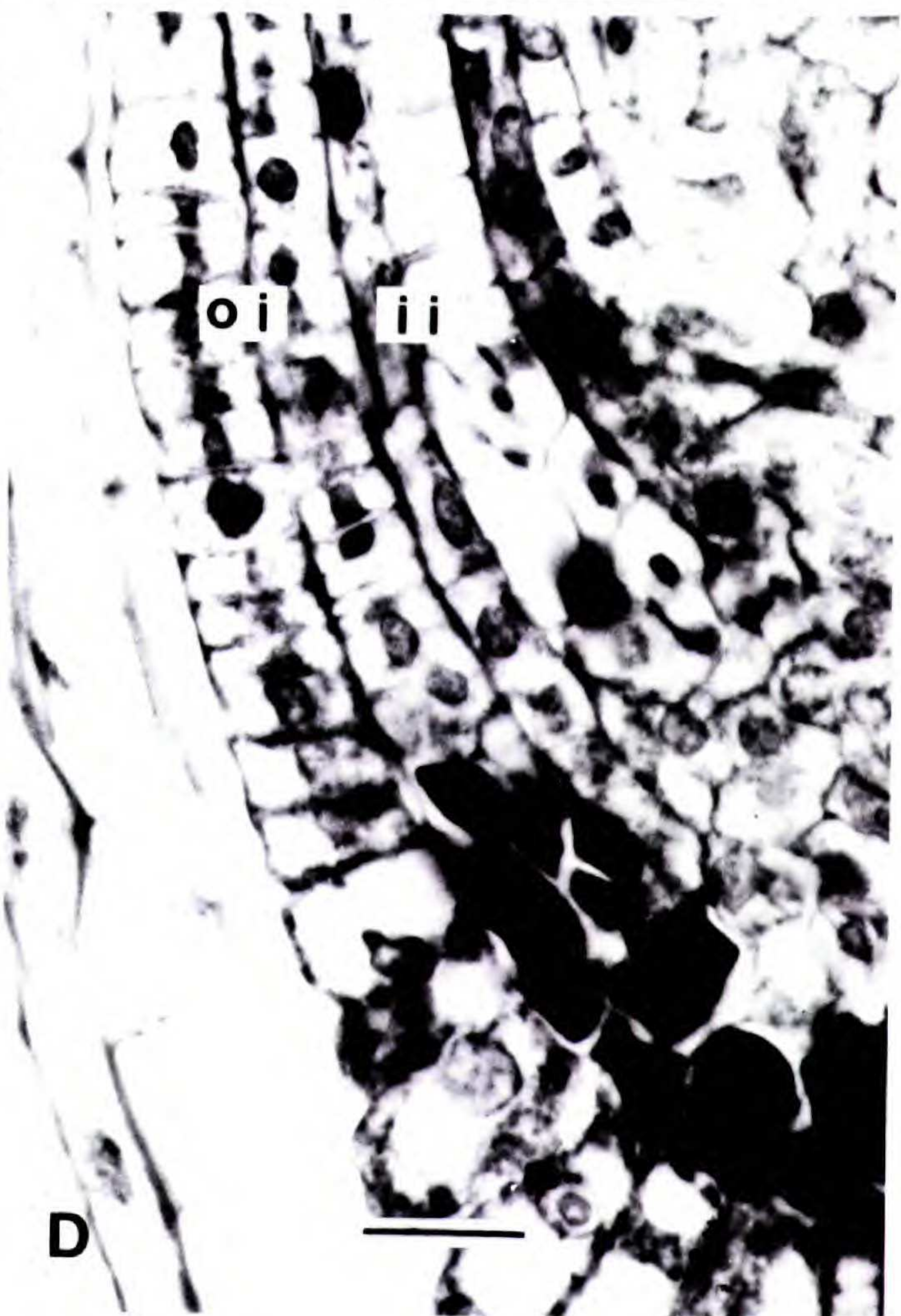
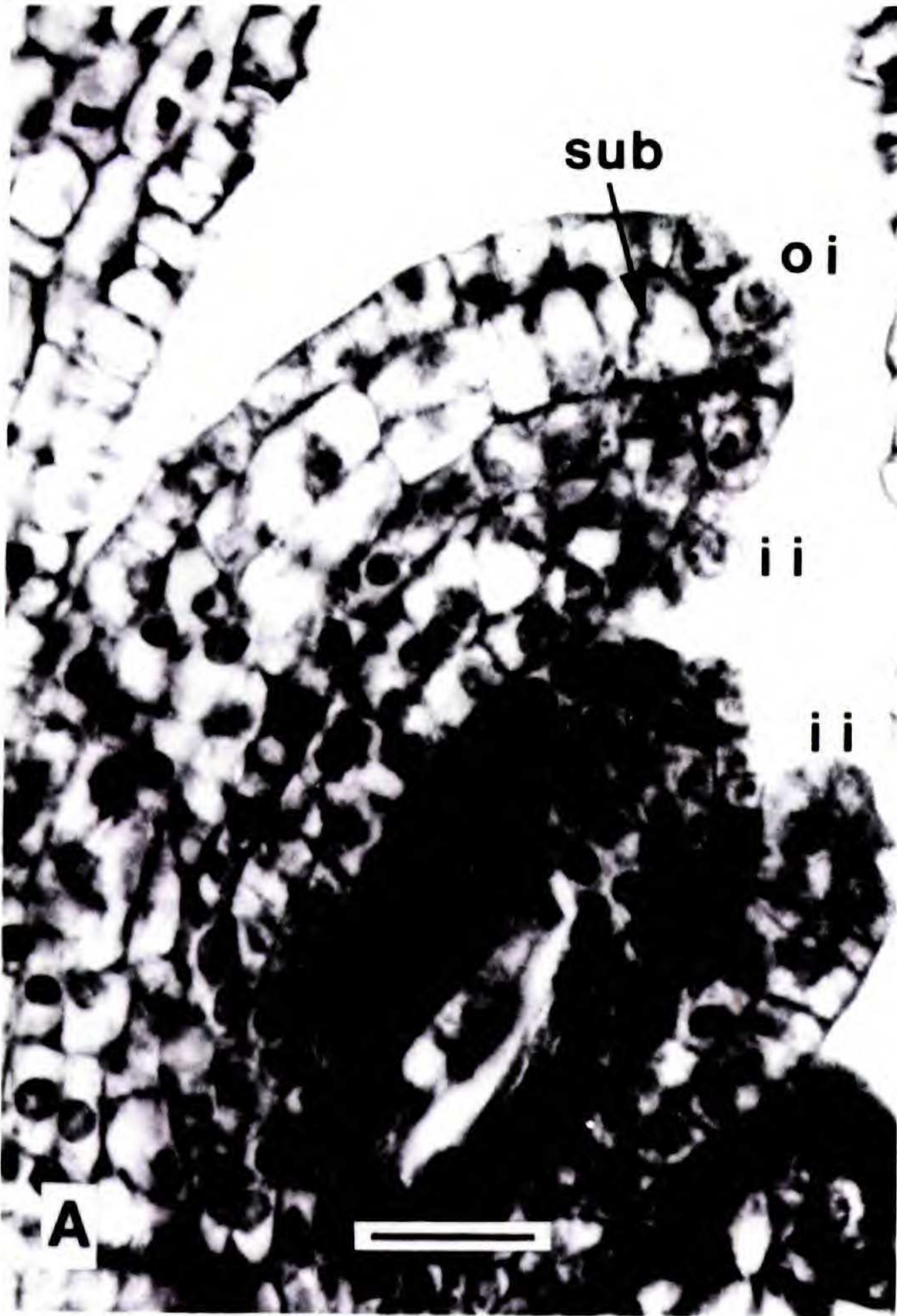


FIGURE 8. *Oenothera flava* subsp. *flava*.—A–C. Median longisections of ovule primordia in progressively successive stages of development, showing that the o.i. is of both dermal and subdermal origin. Note that the derivatives of the dermal initials divide less actively than those of the subdermal ones in the formation of the o.i. Bracket scale = 100 μ m.

subdermal origin with the derivatives of the dermal initials dividing less often than those of the subdermal initials subsequently. In some ovules, the derivatives of the subdermal initials extend close to the tip of the o.i. (Fig. 9B).

Clarkia delicata and *C. tenella*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species (Fig. 9C).

Heterogaura heterandra—Both the i.i. and the o.i. are of dermal origin and two-layered.



TRIBE EPILOBIEAE

Boisduvalia glabella and *B. subulata*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species.

Epilobium canum and *E. ciliatum*—Both the i.i. and the o.i. are of dermal origin and two-layered in both species (Fig. 9D).

DISCUSSION

In Table 1 the results of this study on the histogenesis of integuments are presented comparatively. Although all Onagraceae have a two-layered i.i. of dermal origin, four different types of o.i. are recognized with respect to mode of initiation and subsequent growth. These are found in, respectively, 1) *Lopezia* (Lopezieae), *Fuchsia* (Fuchsieae), and *Circaea* (Circaeae), in which the o.i. is of subdermal origin, and the derivatives of the subdermal initials reach the tip of the o.i. (Fig. 10A); 2) *Oenothera* and *Stenosiphon* (Onagreae), in which the o.i. is of both dermal and subdermal origin, and the derivatives of the subdermal initials extend beyond the middle of the o.i. (Fig. 10B); 3) *Hauya* (Hauyeae) and *Calylophus* and *Gaura* (Onagreae), in which the o.i. is both dermal and subdermal origin, and the derivatives of the subdermal initials are confined to the basal part of the o.i. (Fig. 10C); and 4) *Ludwigia* (Jussiaeae), *Boisduvalia* and *Epilobium* (Epilobieae), and *Camissonia*, *Gayophytum*, *Gongylocarpus*, and *Xylonagra* (Onagreae), in which the o.i. is of dermal origin and mostly two-layered (Fig. 10D).

In angiosperms, the i.i. is almost always of fully dermal derivation and mostly two or three cells thick (Bouman, 1974, 1984); Euphorbiaceae is the only family in which a subdermally initiated i.i. is reported (Bor & Bouman, 1974). Therefore, we could conclude that most Onagraceae have a generalized i.i. with respect to histogenesis and thickness. The amplification in thickness of the i.i. because of periclinal cell divisions, which often is characteristic of *Ludwig-*

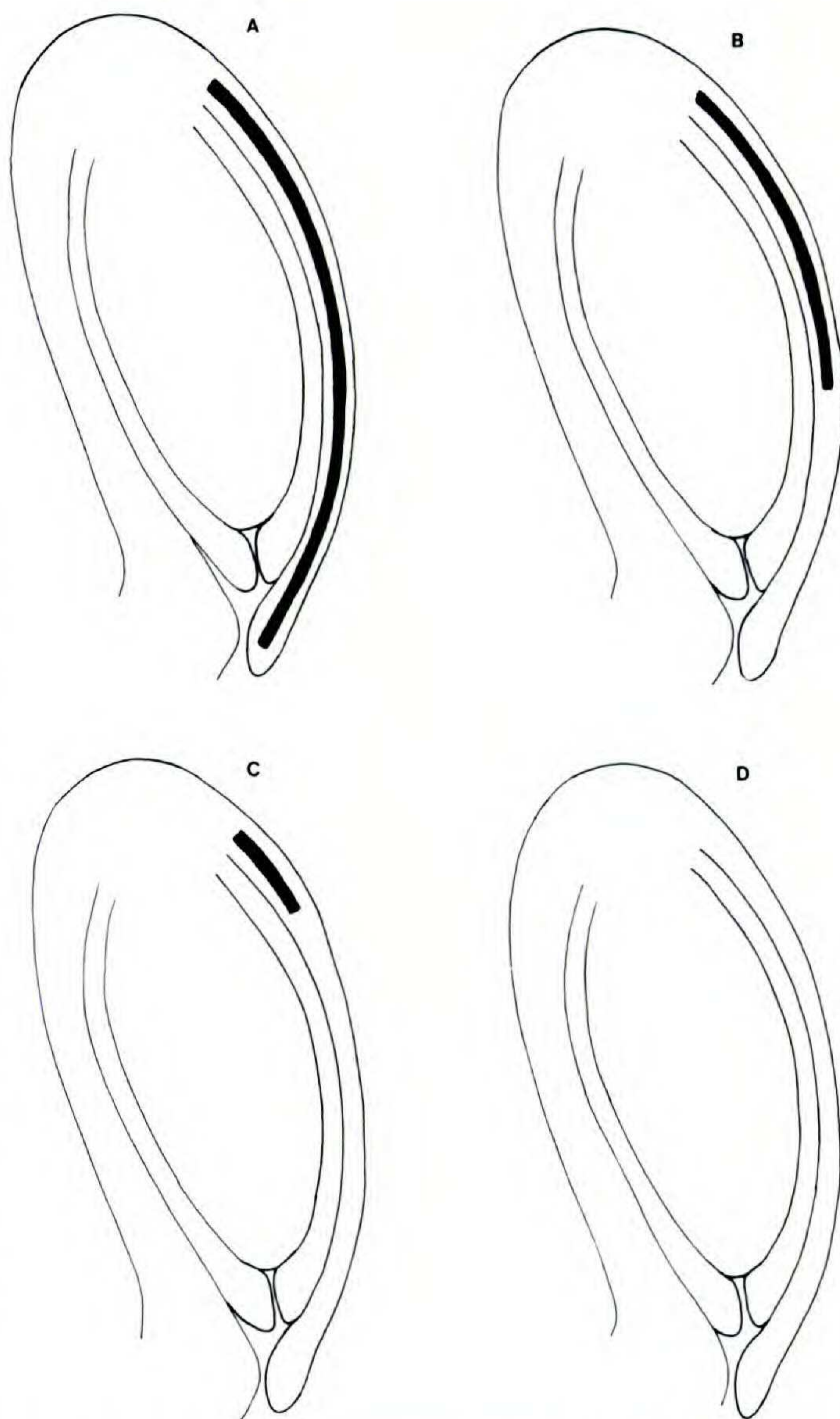


FIGURE 10. Diagrams illustrating four different types of the o.i. with respect to the developmental mode. —A. The o.i. is of subdermal origin. —B. The o.i. is of both dermal and subdermal origin with the derivatives of the subdermal initials dividing more actively than those of the dermal ones. —C. The o.i. of both dermal and subdermal origin with the derivatives of the dermal initials dividing more often than those of the subdermal ones. —D. The o.i. is of dermal origin.

ia, would in that case be interpreted as a secondary characteristic (Bouman, pers. comm.).

Bouman (1974, 1984) has postulated that the most primitive type of angiospermous ovule has

FIGURE 9. A. *Circaea cordata*. Median longisection of a growing ovule, showing that the o.i. is of subdermal origin and the derivatives of the subdermal initials reach up to the tip of the o.i. —B. *Stenosiphon linifolius*. Longisection of apical part of integuments. Note that, since the o.i. is of both dermal and subdermal origin, a certain part of the o.i. is made up of derivatives of both the dermal and subdermal initials. In this ovule, the derivatives of the subdermal initials extend close to the tip of the o.i. —C. *Clarkia tenella*. Median longisection of a growing ovule showing two-layered i.i. and o.i. of dermal origin. —D. *Epilobium ciliatum*. Longisection of a basal part of a developed ovule showing two-layered i.i. and o.i. of dermal origin. sub, derivatives of the subdermal initials. Scales = 20 μ m.

a subdermally initiated o.i. and that thick o.i.'s are more primitive than thinner ones. In light of Bouman's principles, the histogenesis of the o.i.'s of *Lopezia*, *Fuchsia*, and *Circaea* would be considered the most primitive found in Onagraceae, because in these genera the o.i. is entirely of subdermal origin. At least some species of all three genera have the original basic chromosome number for the family, $n = 11$, and generalized chromosome structure (Kurabayashi et al., 1962; Raven, 1979). As indicated by Eyde and Morgan (1973), *Lopezia*, *Fuchsia*, and *Circaea* have no evident direct relationship to one another. For example, although both have reduced numbers of flower parts, *Lopezia* differs from *Circaea* in its anther disposition and nectary morphology. *Fuchsia*, despite its mostly red, bird-pollinated flowers and unique fleshy fruits, may be the modern genus closest to the ancestors of most Onagraceae. The pattern of histogenesis of its integuments is in accordance with such a conclusion.

The tribe Onagreae, with ten genera, exhibits three patterns with respect to the histogenetic characters of integuments (see Table 1). Based on Bouman's (1974, 1984) postulates, *Oenothera* and *Stenosiphon* are more primitive than other members of the tribe in that their o.i. retains a stronger tendency to entirely subdermal initiation (see Fig. 10B). *Calylophus* and *Gaura* appear to be more specialized than *Oenothera* and *Stenosiphon*, and less specialized than other Onagreae, in that their o.i. still retains a weak tendency to an entirely subdermal initiation (see Fig. 10C). The remaining six genera, *Camissonia*, *Gayophytum*, *Gongylocarpus*, *Xylonagra*, *Clarkia*, and *Heterogaura*, in which the o.i. has no tendency to a subdermal initiation (see Fig. 10D), constitute a third group, which on the basis of this feature would be considered the most advanced in the tribe.

It is almost certain that the patterns of integumental histogenesis found in these three groups were derived from one in which the o.i. was entirely of subdermal origin, like that which persists in *Fuchsia*, *Lopezia*, and *Circaea*. It is not, however, possible to determine whether they were derived sequentially or independently on the basis of this characteristic alone. *Gongylocarpus* is the only genus of Onagreae that retains the original basic chromosome number for the family, $n = 11$, but it has a highly specialized pattern of ovary development (Carlquist & Raven, 1966). If it is an offshoot from the line leading to *Camissonia*, *Gayophytum*, and *Xylonagra* (Raven,

1964, 1969), then, since all of these genera have identical specialized patterns of integumentary histogenesis in agreement with their distinctive stigma morphology, it would be implied that there is no direct relationship between this line and other Onagreae. Certainly, these relationships make it appear that the reduced basic chromosome number, $n = 7$, must have been derived separately in this line and in the other parts of the tribe.

The large genus *Oenothera* (about 125 species) is identical to the monotypic *Stenosiphon* in the pattern of histogenesis of its integuments, as it is in stigma morphology and other features. Thus the close relationship between these genera first postulated by Raven (1964) is confirmed, but the relationship between these genera and others within the tribe remains obscure. The basic chromosome number, $n = 7$, in these genera certainly seems to have evolved independently from the same number in other genera of Onagreae.

Clarkia and *Heterogaura* share the specialized feature of the o.i. with the first group discussed above. If they are directly related to *Calylophus* and *Gaura*, as claimed by Raven (1964, 1969) on the basis of the thick partitions that divide the sporogenous tissue of their anthers into packets, it would have to be assumed that the pattern of development of their o.i.'s was independently derived from that in the "*Gongylocarpus*—group"; if not, then their specialized anthers and stigmas must have evolved within that group.

Hauya ($x = 10$), now placed in a separate tribe Hauyae (Raven, 1979) on the basis of the many features, all apparently retained primitive ones, in which it differs from all genera currently assigned to Onagreae, was formerly grouped with *Calylophus*, *Clarkia*, *Gaura*, and *Heterogaura* on the basis of its divided sporogenous tissue. The histogenesis of its integuments is identical to that in *Calylophus* and *Gaura*, differing sharply from the more advanced condition found in *Clarkia* and *Heterogaura* and the more primitive one in *Oenothera* and *Stenosiphon*. This may indicate that *Calylophus* and *Gaura* (both $x = 7$) were derived from a phylogenetic line separate from that leading to other Onagreae, and that *Hauya* may be a surviving early evolutionary offshoot of that line. The relationships of the different genera of Onagreae and their affinity to *Hauya* will be discussed in more detail in a separate paper focusing on the exact nature of the divided sporogenous tissue in the Onagraceae (Tobe & Raven, 1985).

The remaining two tribes of the family, Jus-

siaeeae (*Ludwigia* only) and Epilobieae (*Epilobium* and *Boisduvalia*), share with six genera of Onagreae the most advanced type of integumentary histogenesis in the family, with a two-layered o.i. of dermal origin. Fundamental floral differences discussed by Eyde (1977, 1978, 1981) make it clear that *Ludwigia* represents a phylogenetic line different from all other Onagraceae, so that it must have evolved its specialized o.i. independently. There appears to be no evidence to suggest a close grouping of Epilobieae with any genera of Onagreae, so that we may assume that a two-layered o.i. of dermal origin evolved independently in it, in the *Gongylocarpus*-line, and perhaps also in *Clarkia*–*Heterogaura*—thus three or even four times within Onagraceae. A similar condition has evolved independently in various angiosperms, as for example, Lactoridaceae among “Polycarpicae” (Bouman, 1971).

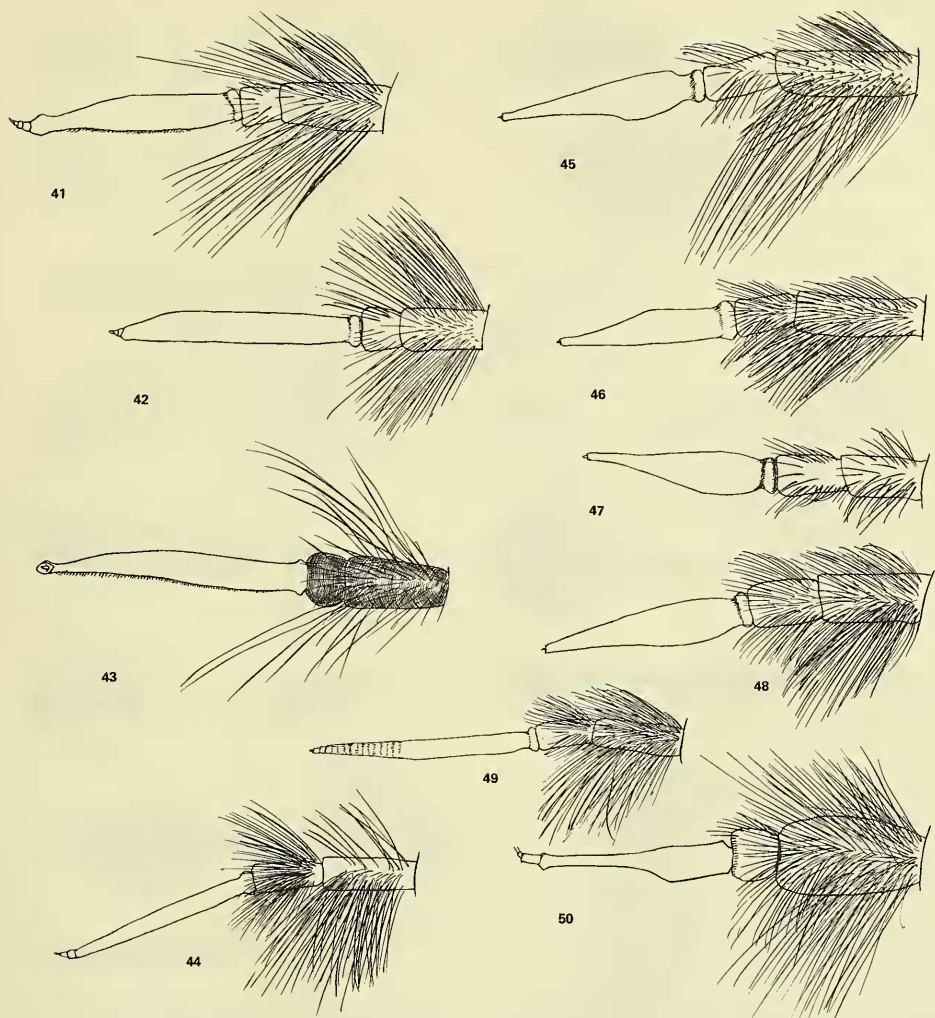
Within the family, *Ludwigia peploides* (sect. *Oligospermum*) is distinct from all other species in having a three-layered o.i. instead of a two-layered one. Eyde (1977), pointing out that sect. *Oligospermum* stands apart from other ludwigias because of its characteristic aerenchymatous tissue surrounding the endocarp, inferred that this section seems to have diverged early from the other ludwigias and developed its own aquatic adaptations. The characteristic developmental mode of its integuments, unique in Onagraceae, constitutes additional evidence supporting his hypothesis.

This comparative study covering the whole family enables us to evaluate the histogenetic characters of integuments. As has been described and seen in Table 1, this character is nearly genus-specific. Even in cases in which the seed coat or testa histology differs from species to species (e.g., in *Gongylocarpus*, Carlquist & Raven, 1966), the mode of initiation and the subsequent growth of the integuments is consistent within a genus. In view of this, detailed comparisons of this character have made it possible to evaluate the affinities of genera and to consider their relative states of advancement.

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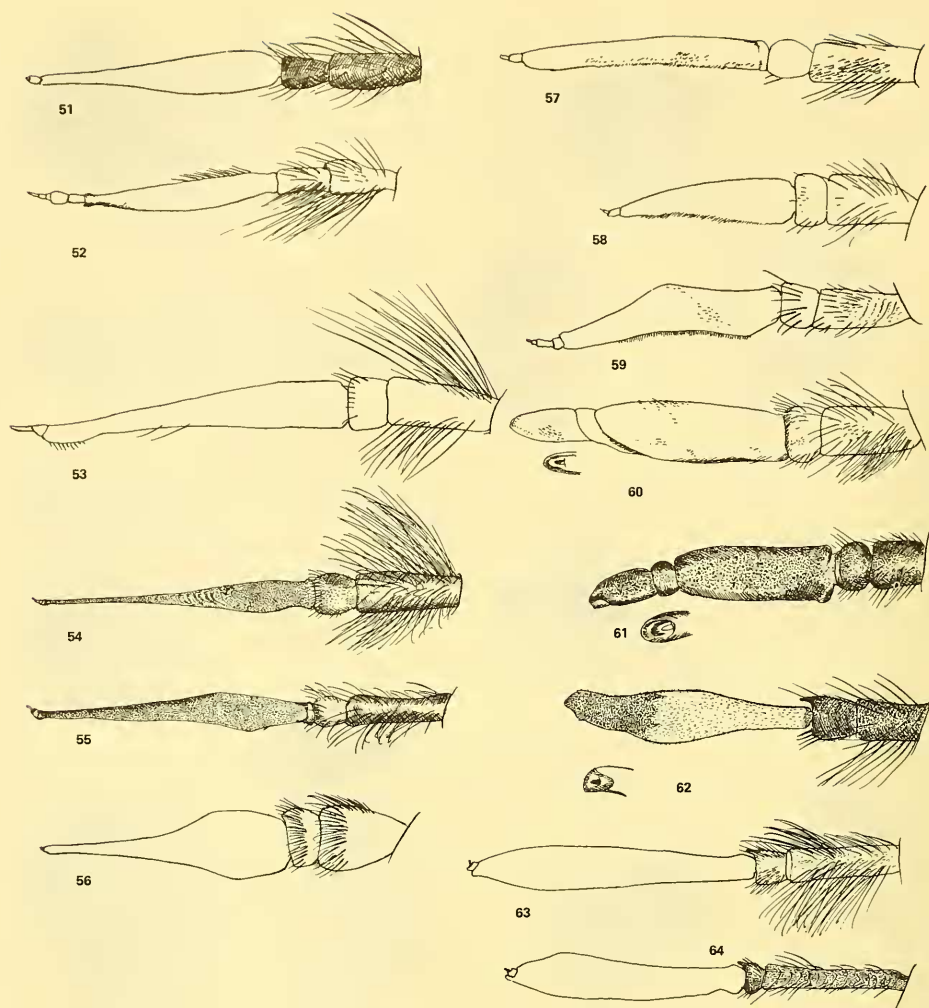
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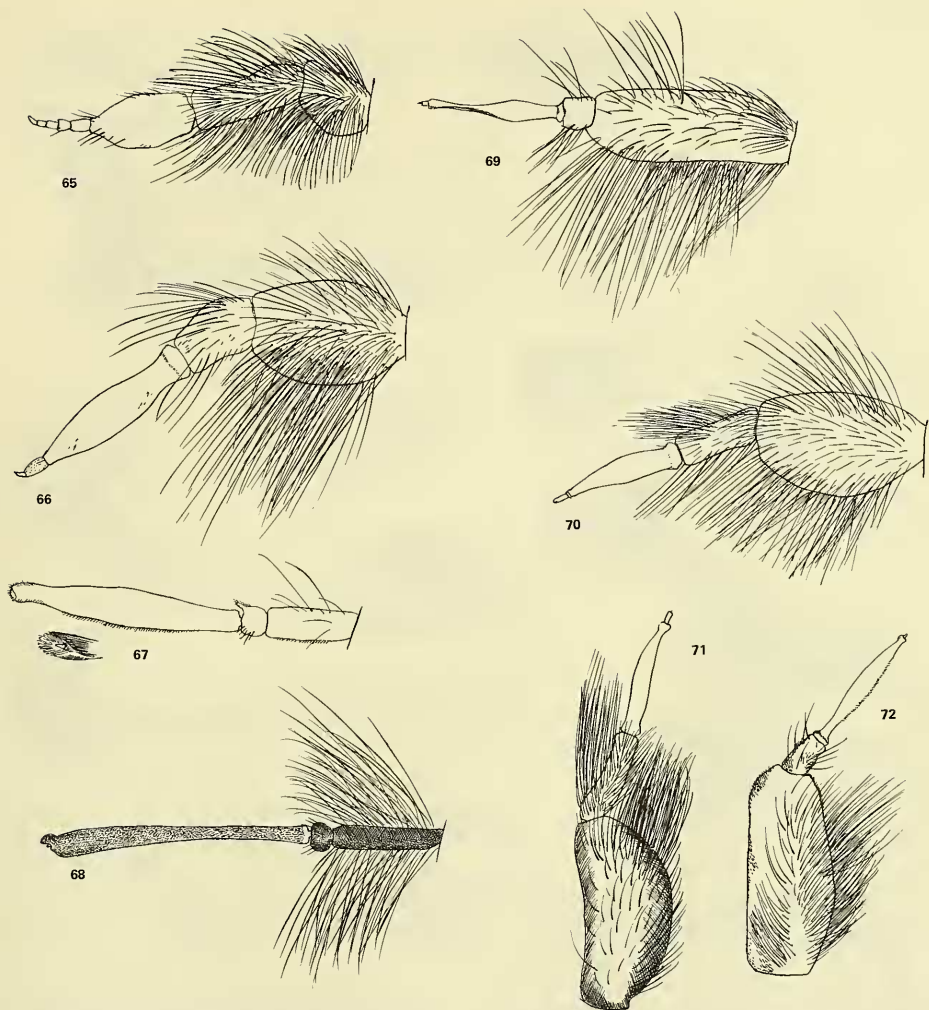
FIGURES 41-50.—41, *Chasmoneura argyropygus* Wiedemann. 42, *Chasmoneura pectoralis* Loew. 43, *Lepidochlanus fimbriatus* Hesse, male, paratype. 44, *Cacoplox griseata* Hull. 45, *Lordotus*

gibbus Loew. 46, *Lordotus zonus* Coquillett. 47, *Lordotus bipartitus* Painter, paratype. 48, *Lordotus diversus* Coquillett. 49, *Euprepina nuda* Hull. 50, *Sericusia* sp.



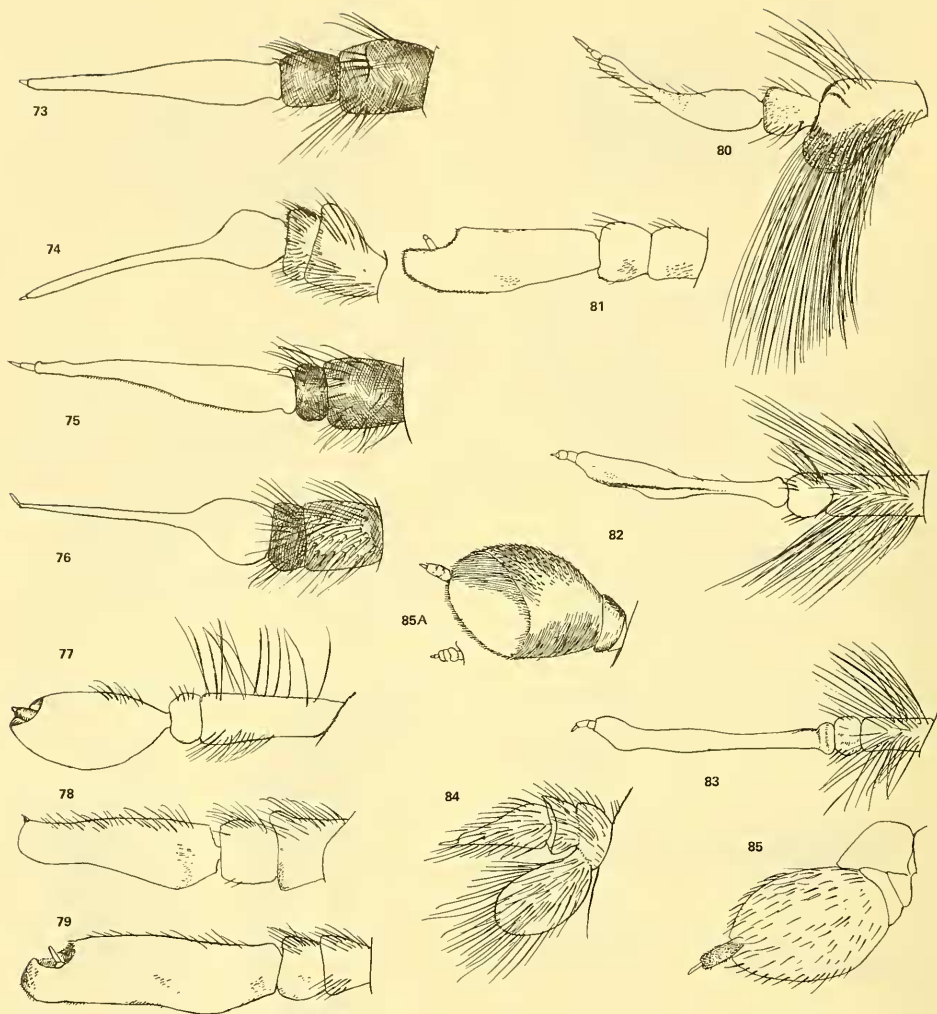
FIGURES 51-64.—51, *Eurycarenum laticeps* Loew. 52, *Eurycarenum dichopticus* Bezzi. 53, *Triploechnus heteroneurus* Macquart. 54, *Heterostylum croceum* Painter, paratype. 55, *Heterostylum robustum* Osten Sacken. 56, *Gyrocraspedum pleskei* Becker. 57, *Crocidium* sp. 58, *Crocidium namaquense*

Hesse. 59, *Crocidium phaeopteralis* Hesse. 60, *Desmatomyia binotata* Painter, paratype. 61, *Desmatomyia anomala* Williston. 62, *Hyperusia soror* Bezzi. 63, *Corsomyza brevicornis* Hesse. 64, *Corsomyza simplex* Wiedemann.



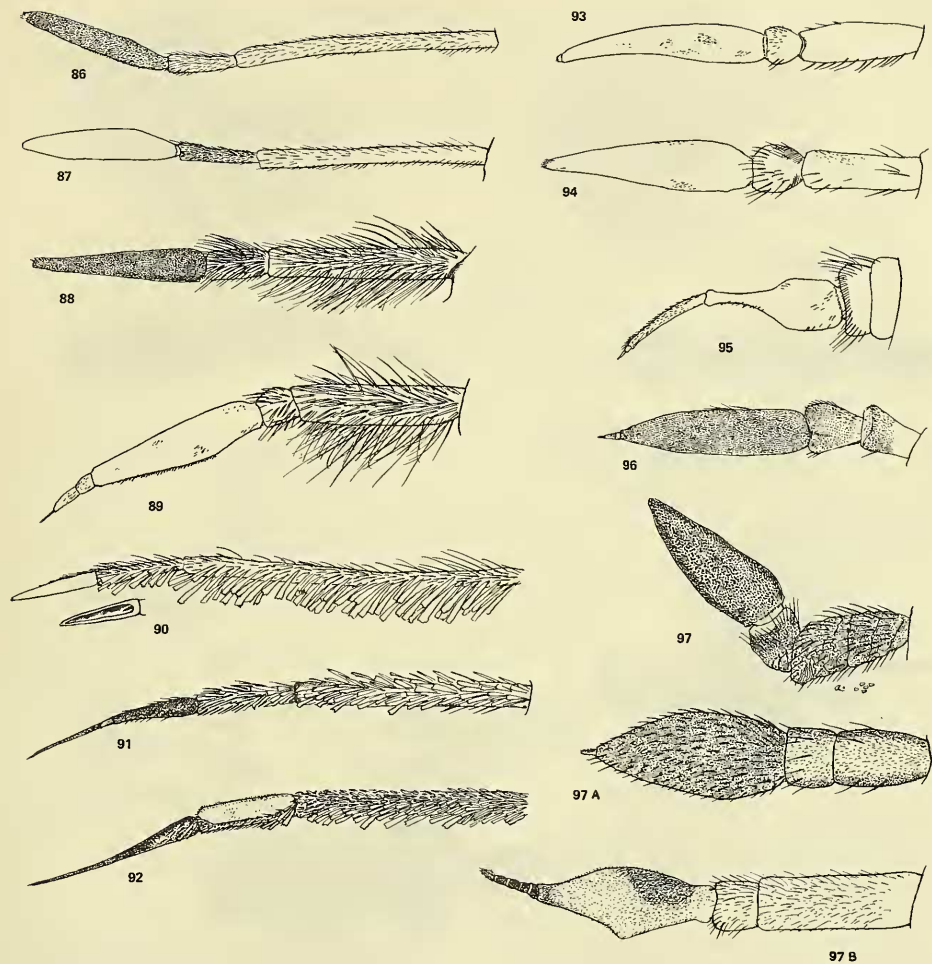
FIGURES 65-72.—65, *Aldrichia erhmanii* Coquillett. 66, *Conophorus cristatus* Painter. 67, *Megapalpus capensis* Wiedemann. 68, *Corsomyza nigripes* Wiedemann, male. 69, *Conophorus virescens* Fabri-

cius. 70, *Conophorus fenestratus* Osten Sacken. 71, *Conophorus fenestratus* Osten Sacken, male, dorsal aspect. 72, *Conophorus virescens* Fabricius, male, dorsal aspect.



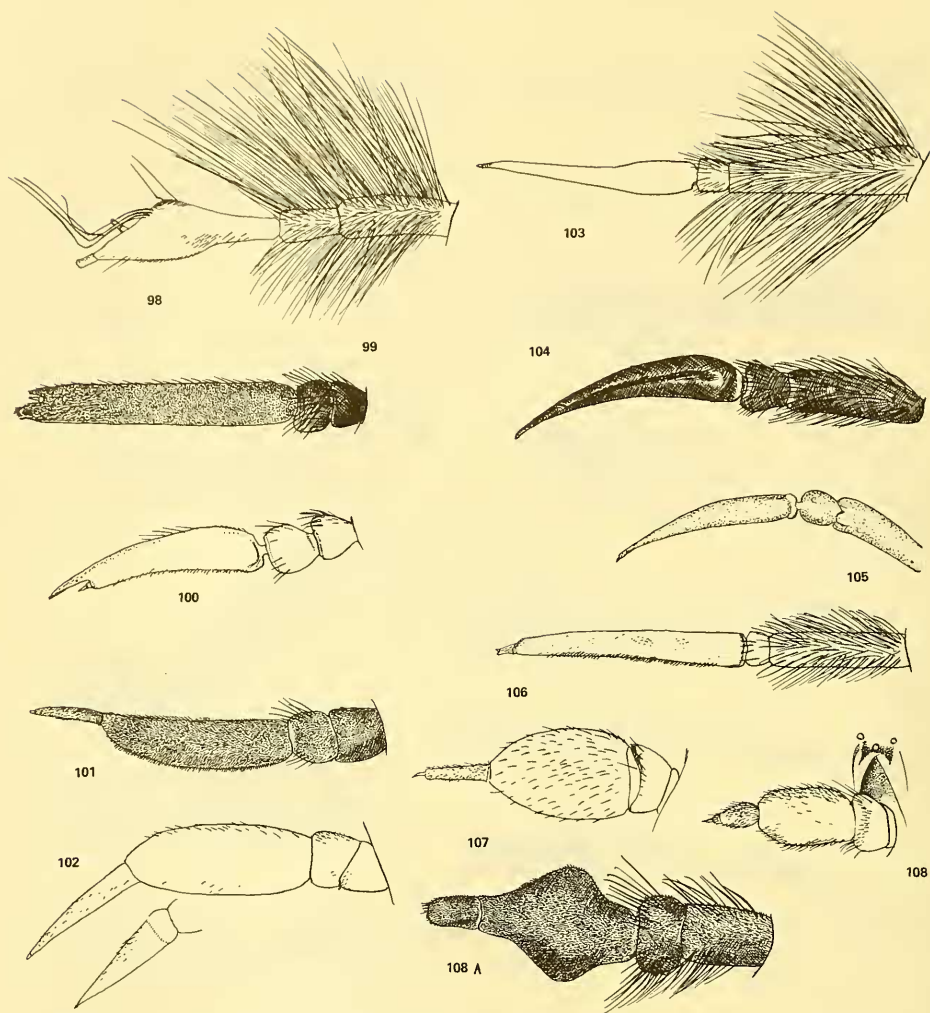
FIGURES 73-85A.—73, *Cytherea obscura* Fabricius, medial aspect. 74, *Callostoma fascipenne* Macquart, dorsal aspect. 75, *Cytherea (Chalcochiton) pallasi* Loew. 76, *Callostoma fascipenne* Macquart, lateral aspect. 77, *Oligodranes cincturus* Coquillett. 78, *Usia florea* Fabricius, male. 79,

Usia aenea Rossi. 80, *Oniromyia pachyceratus* Bigot. 81, *Apolysis druivas* Melander. 82, *Pantarbates capito* Osten Sacken. 83, *Pantarbates willistoni* Osten Sacken. 84, *Xenoprosopa paradoxa* Hesse, after Hesse. 85, *Apystomyia elinguis* Melander, paratype. 85A, *Glabellula* sp.



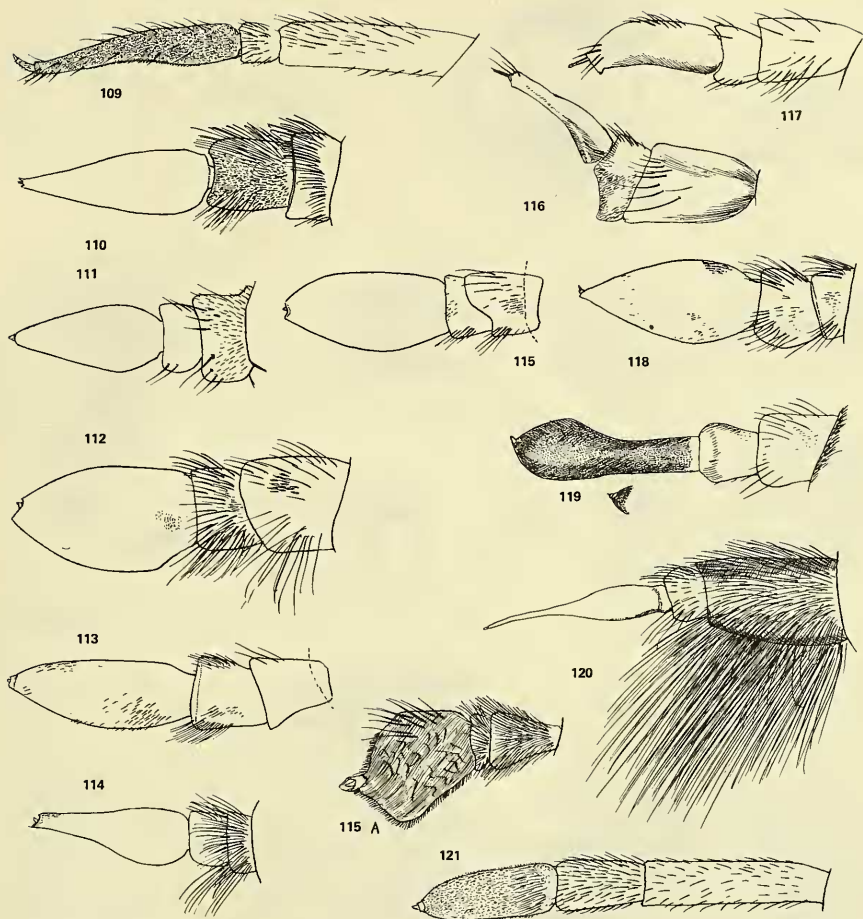
FIGURES 86-97B.—86, *Systropus quadripunctata* Seguy. 87, *Systropus angulatus* Karsch. 88, *Cyrtomyia chilensis* Paramonov. 89, *Marmasoma sumptuosa* White. 90, *Lepidophora lepidocera* Wiedemann. 91, *Toxophora amphitea* Walker, male, lateral aspect. 92, *Toxophora amphitea*

Walker, male, dorsal aspect. 93, *Dolichomyia gracilis* Williston. 94, *Dolichomyia* sp., Chile. 95, *Cyrtomorpha paganica* White. 96, *Heterotropus aegyptiacus* Paramonov. 97, *Zaclava* sp. 97A, *Pro-rates claripennis* Melander. 97B, *Apatomyza punctipennis* Wiedemann, holotype.



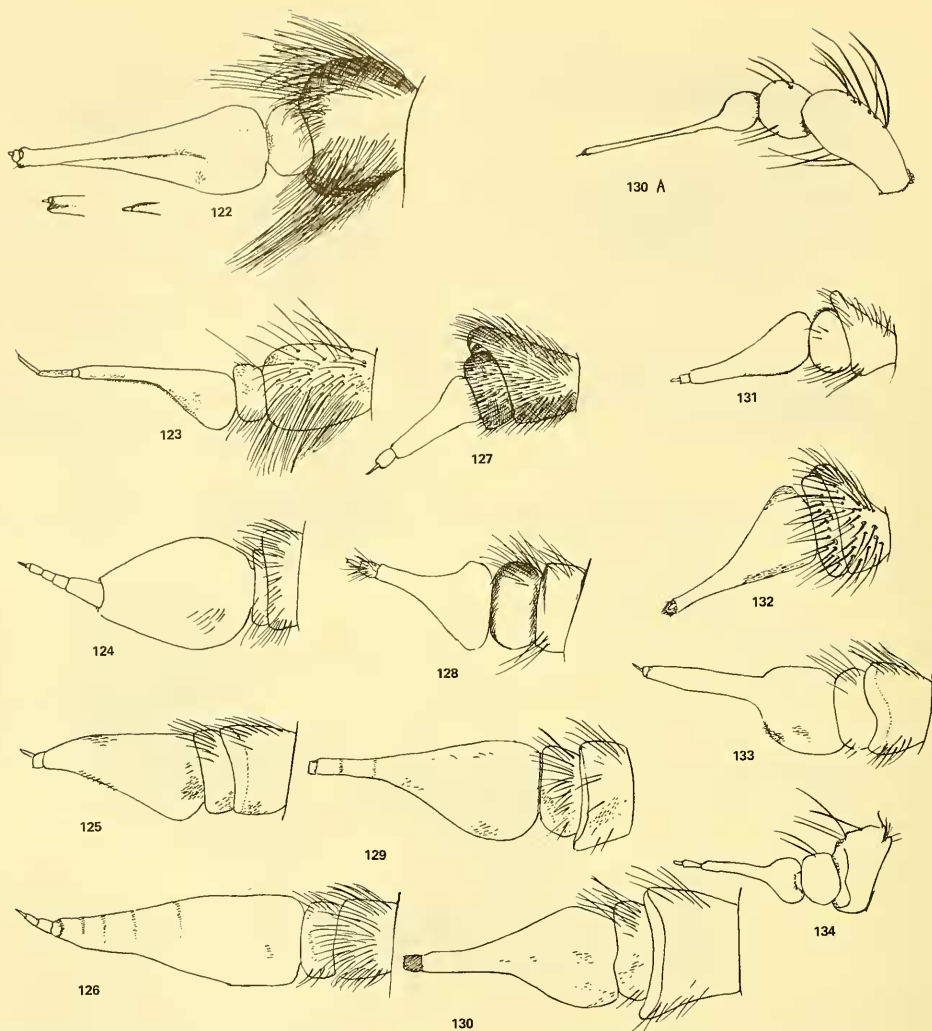
FIGURES 98-108A.—98, *Acreotrichus gibbicornis* Macquart. 99, *Phthiria* sp. 100, *Phthiria gaedei* Wiedemann, after Engel. 101, *Mythicomyia monacha* Melander, paratype. 102, *Mythicomyia armada* Cresson, paratype. 103, *Pseudoamictus*

heteropterus Wiedemann. 104, *Geron* sp., New Mexico. 105, *Geron gibbosus* Olivier. 106, *Amictogeron meromelas* Hesse, paratype. 107, *Empidideicus eflatouni* Engel. 108, *Empidideicus humilis* Melander. 108A, *Caenotus hospes* Melander.



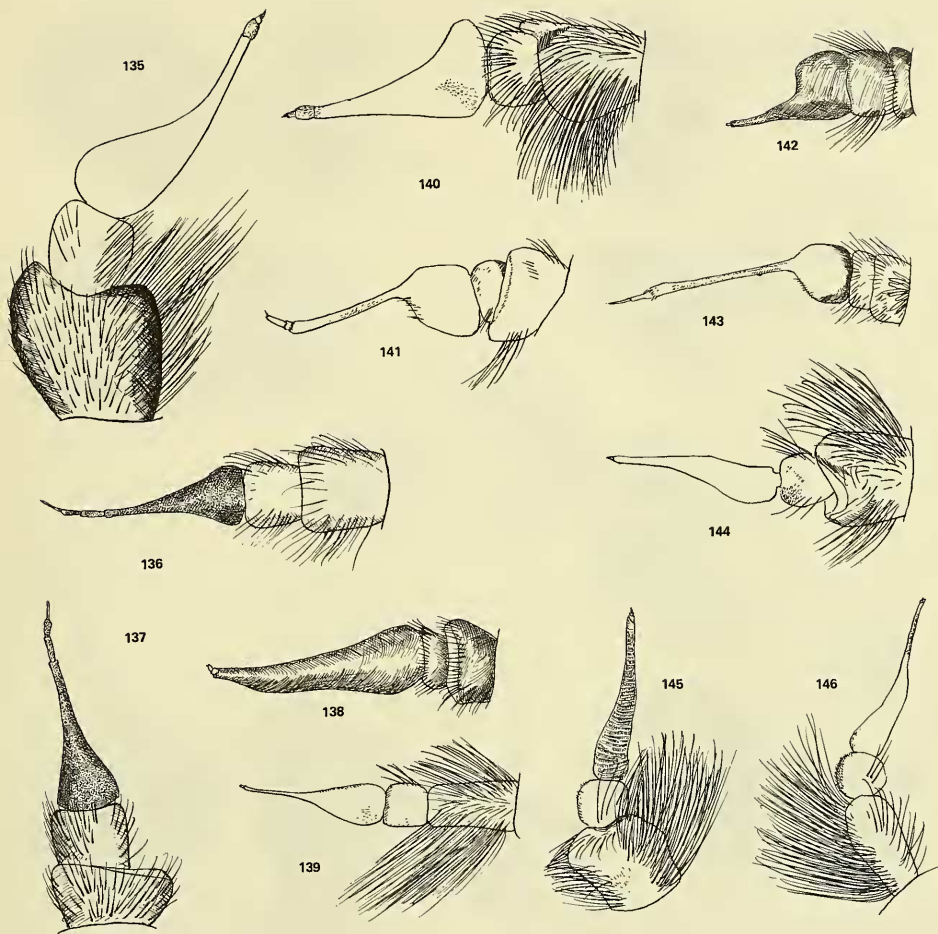
FIGURES 109-121.—109, *Amictus validus* Loew. 110, *Amphicosmus cincturus* Williston. 111, *Pantostomus tinctellipennis* Hesse, paratype. 112, *Paracosmus morrisoni* Osten Sacken. 113, *Tomomyza anthracoides* Wiedemann. 114, *Amphicosmus elegans* Coquillett. 115, *Tomomyza philoxera* Hesse, paratype. 115A, *Proracthes longirostris*

Bezzi. 116, *Cyllenla marginata* Loew, dorsal aspect. 117, *Cyllenla marginata* Loew, lateral aspect. 118, *Metacosmus nitidus* Cole. 119, *Paracosmus (Actherosia) rubicundus* Melander. 120, *Peringueyimyia capensis* Wiedemann. 121, *Neosardus principius* Roberts.



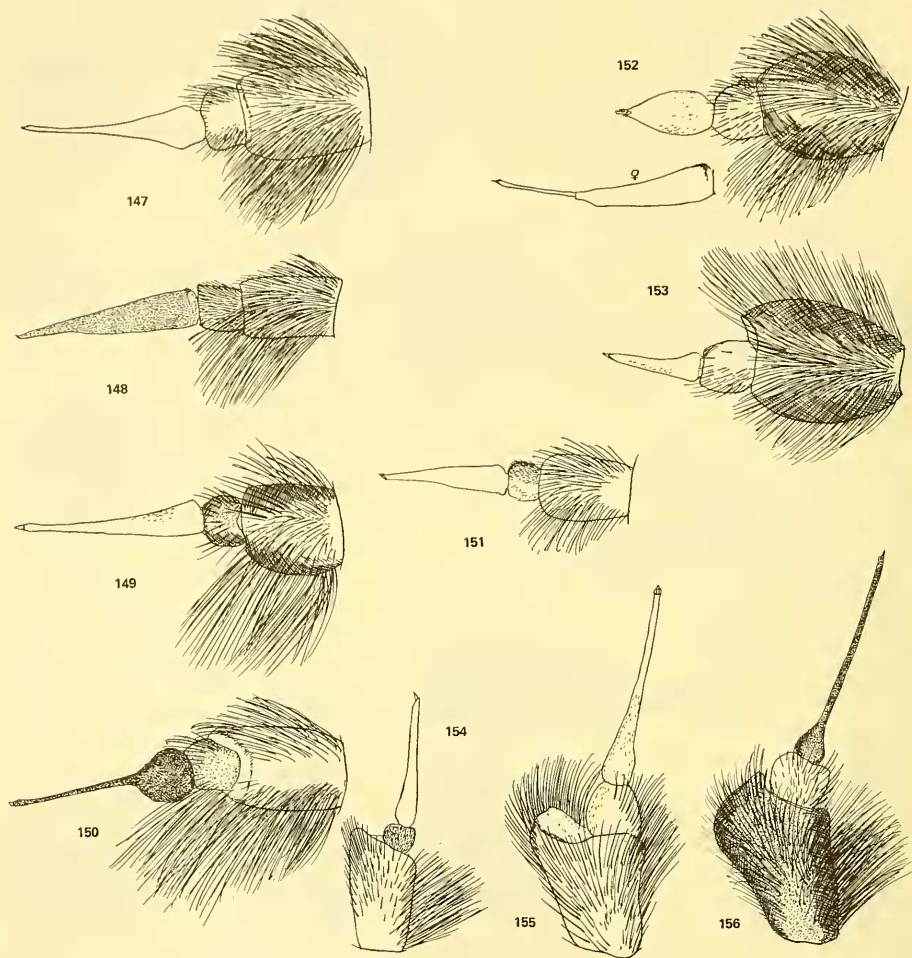
FIGURES 122-134.—122, *Ogcodocera leucoprocta* Wiedemann. 123, *Pteraulax setaria* Hesse. 124, *Eucessia* sp. 125, *Plesiocera psammophila* Hesse, paratype. 126, *Aphoebantus* sp., Texas. 127, *Plesiocera algira* Macquart. 128, *Xeramoeba gracilis* Bowden, paratype. 129, *Epacmoides bi-*

umbonatum Bezzi. 130, *Prorostoma integrum* Bezzi. 130A, *Lomatia (Canariellum) brunnipennis* Macquart, after Engel. 131, *Stomylomyia europae* Loew. 132, *Coryprosopa lineata* Hesse, paratype. 133, *Desmatoneura argentifrons* Williston. 134, *Petrrossia hesperus* Rossi, after Engel.



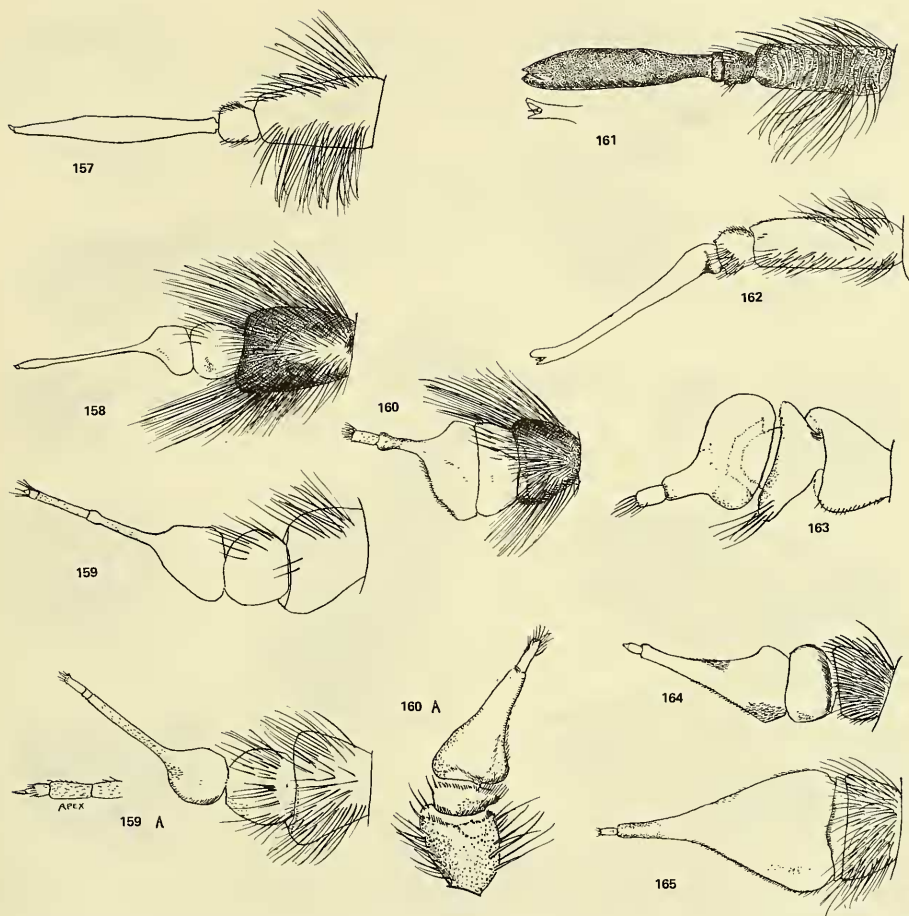
FIGURES 135-146.—135, *Myonema humilis* Roberts, dorsal aspect. 136, *Antonia suavissima* Loew. 137, *Antonia suavissima* Loew, dorsal aspect. 138, *Antonia* sp., Australia. 139, *Lomatia* sp., So. Africa. 140, *Myonema humilis* Roberts. 141,

Epacmus sp. 142, *Docidomyia puellaris* White. 143, *Epacmus litus* Coquillett. 144, *Lomatia belzebul* Fabricius. 145, *Lomatia belzebul* Fabricius, dorsal aspect. 146, *Lomatia* sp., So. Africa, dorsal aspect.



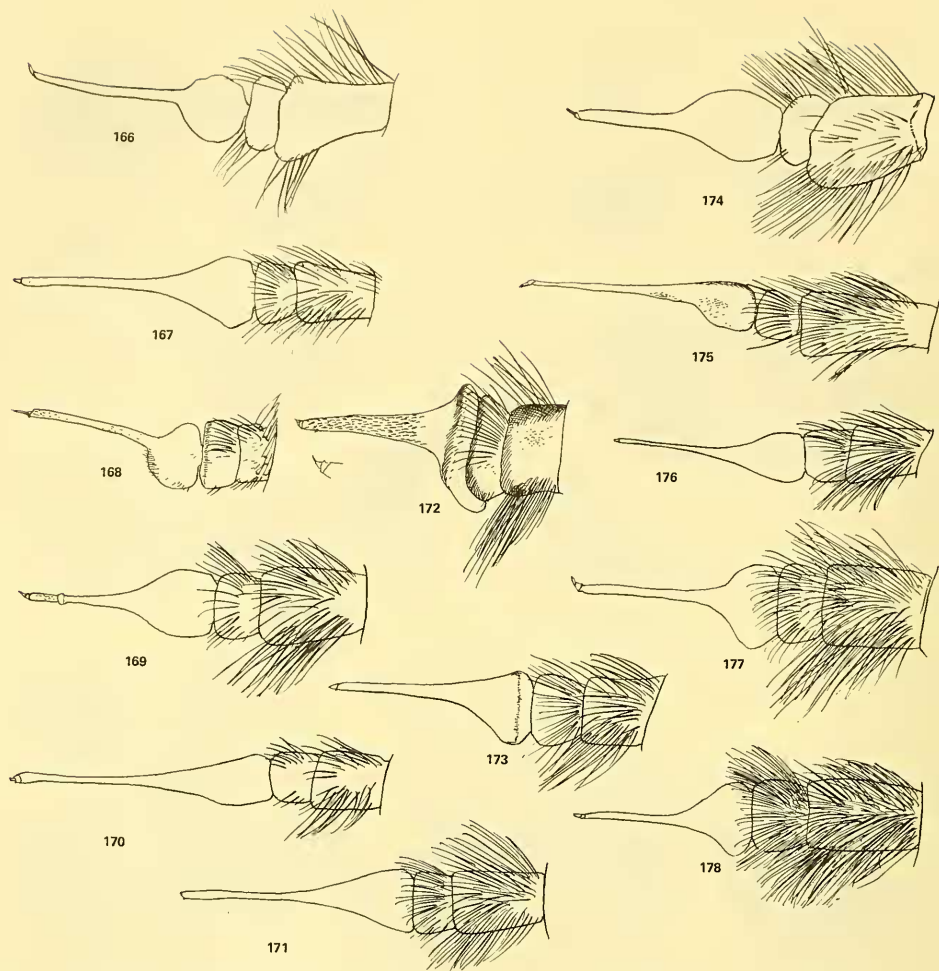
FIGURES 147-156.—147, *Lyophlaeba* sp. 148, *Ylaoia pegasus* Wiedemann. 149, *Doddosia picta* Edwards. 150, *Comptosia (Paradosia) tendens* Walker. 151, *Lyophlaeba (Macrocondyla) montana* Philippi. 152, *Oncodosia planus* Walker, male, female. 153, *Onc-*

dosia planus Walker, dorsal aspect. 154, *Lyophlaeba (Macrocondyla) montana* Philippi, dorsal aspect. 155, *Doddosia picta* Edwards, dorsal aspect. 156, *Comptosia fascipennis* Macquart, dorsal aspect.



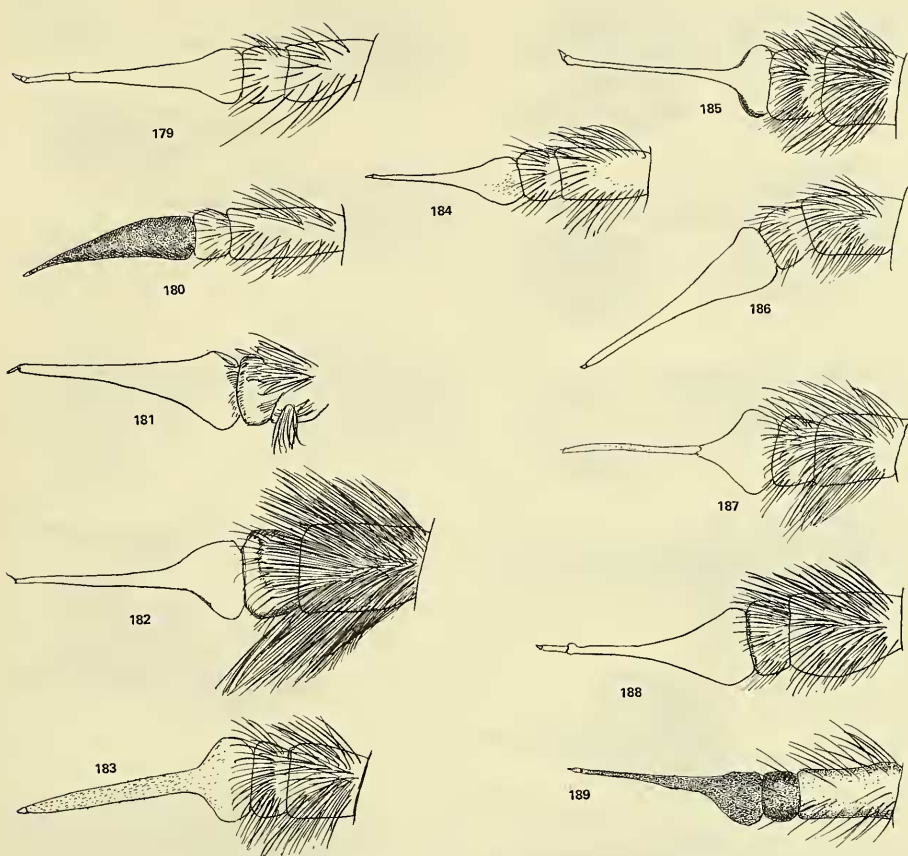
FIGURES 157-165.—157, *Lyophlaeba lugubris* Rondani. 158, *Comptosia ocellata* Newman, male. 159, *Anthrax argyropygus* Wiedemann. 159A, *Anthrax analis* Say. 160, *Dicranoclista vandykei* Coquillett. 160A, *Anthrax (Satyramoeba) etrusca*

Fabricius, after Engel. 161, *Lyophlaeba* sp. 162, *Lyophlaeba* sp., dorsal aspect. 163, *Anthrax aethiops* Fabricius, after Engel. 164, *Walkeromyia luridus* Walker. 165, *Walkeromyia* sp., male, Nova Teutonia.



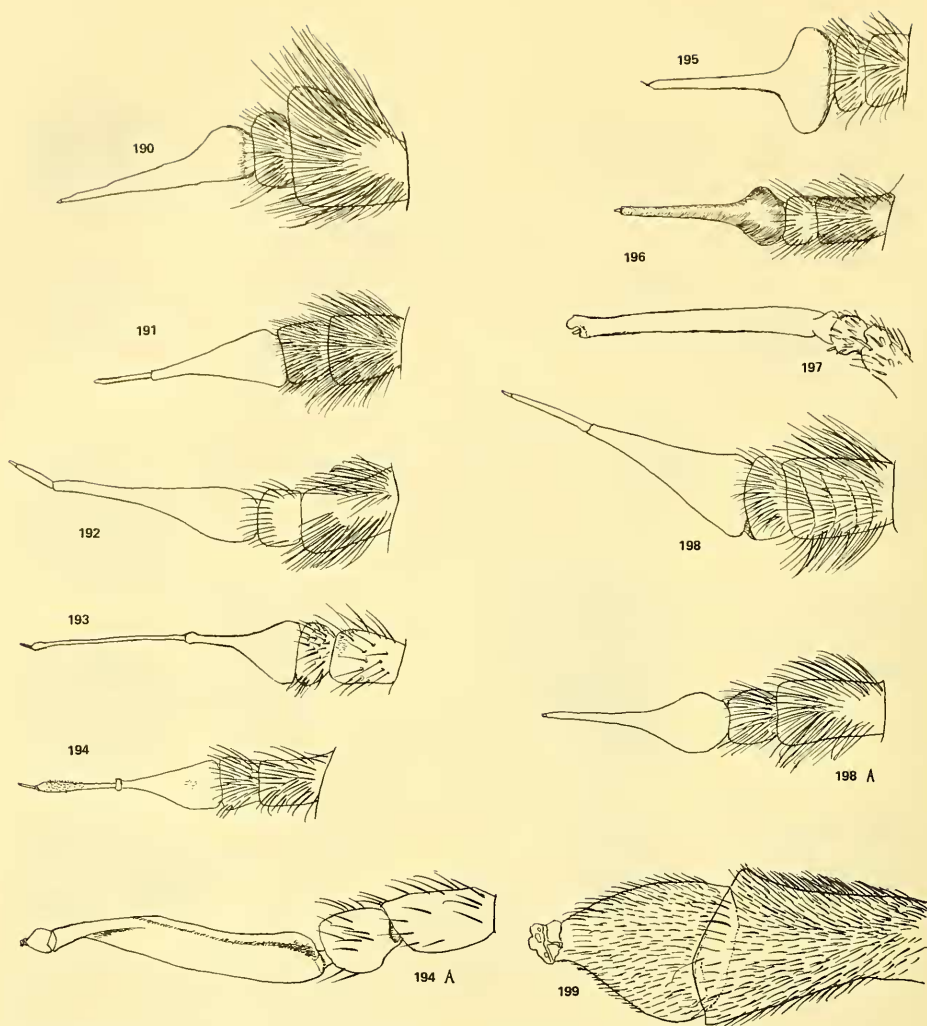
FIGURES 166-178.—166, *Oestranthrax obesus* Loew. 167, *Neodiplocampta paradoxus* Jaenicke. 168, *Mancia nana* Coquillett. 169, *Thyridanthrax afer* Fabricius. 170, *Chrysanthrax cypris* Meigen. 171, *Thyridanthrax perspicillaris* Loew. 172, *Astrophanes adonis* Osten Sacken. 173, *Deusopora*

sapphirina Hull. 174, *Marleyimyia natalensis* Hesse, after Hesse. 175, *Cyananthrax cyanoptera* Wiedemann. 176, *Paravilla castanea* Jaenicke. 177, *Hemipenthes morio* Linné. 178, *Hemipenthes maurus* Linné.



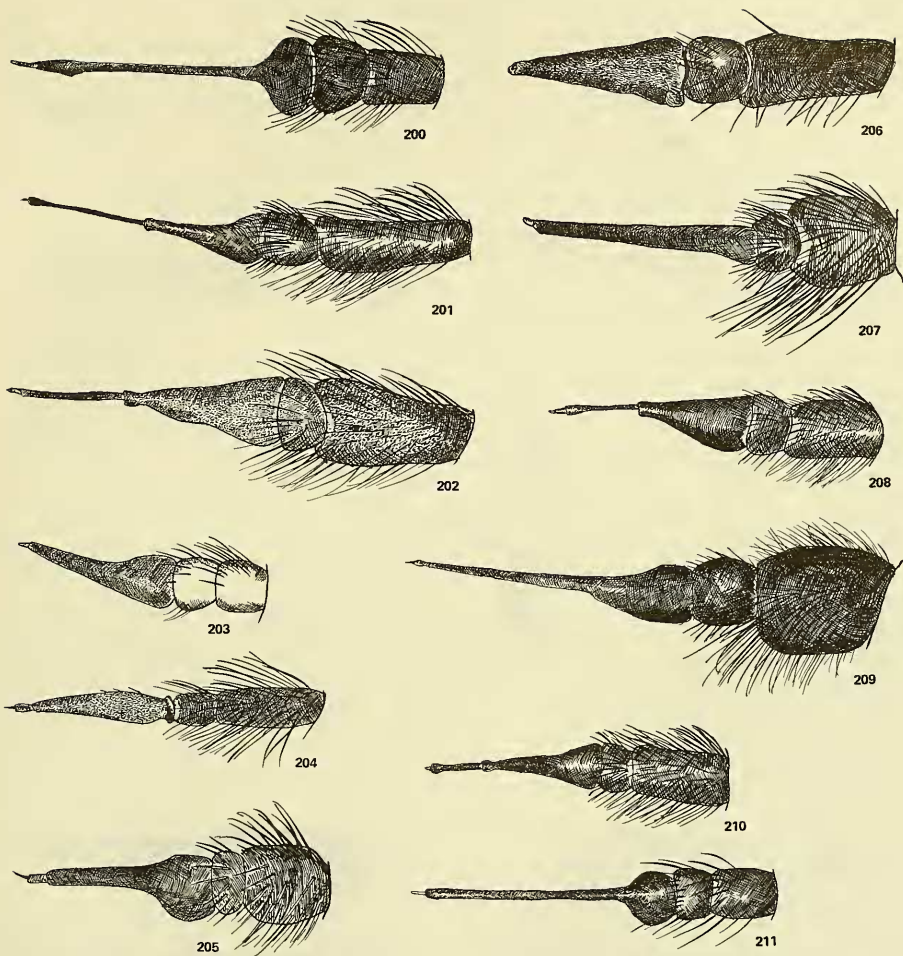
FIGURES 179-189.—179, *Chrysanthrax edititia* Say. 180, *Poecilanthrax effrenus* Coquillett. 181, *Villa cingulata* Wiedemann. 182, *Villa alternata* Say. 183, *Hemipenthes lepidotus* Osten Sacken. 184, *Paravilla xanthina* Painter. 185, *Hemipenthes* sp.,

near *sinuosa* Wiedemann. 186, *Dipalta serpentina* Osten Sacken. 187, *Hemipenthes velutinus* Meigen. 188, *Thyridanthrax pertusa* Loew. 189, *Neodiplocamptia (Agitonia) sepia* Hull.



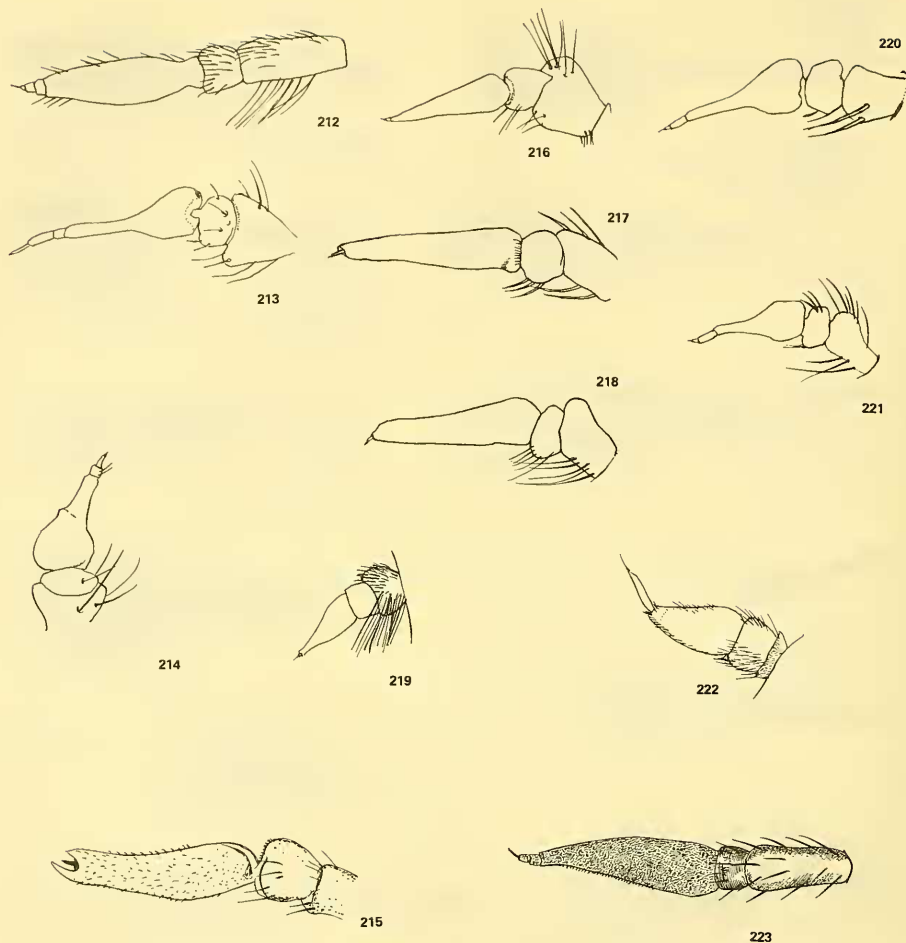
FIGURES 190-199.—190, *Poecilanthrax californicus* Cole, dorsal aspect. 191, *Litorrhynchus lar* Fabricius. 192, *Hyperalonia morio* Fabricius. 193, *Isotamia daveyi* Bezzi, paratype of *Ogilviella tridentata* Paramonov. 194, *Heteralonia kaokoensis* Hesse. 194A, *Diatropomma carcassoni* Bowden,

after Bowden. 195, *Diplocamptia secunda* Paramonov. 196, *Pseudopenthes fenestrata* Roberts. 197, *Exoprosopa subfasciata* Engel, after Engel. 198, *Exoprosopa jacchus* Fabricius. 198A, *Poecilanthrax californicus* Cole, lateral aspect. 199, *Diatropomma carcassoni* Bowden, after Bowden.



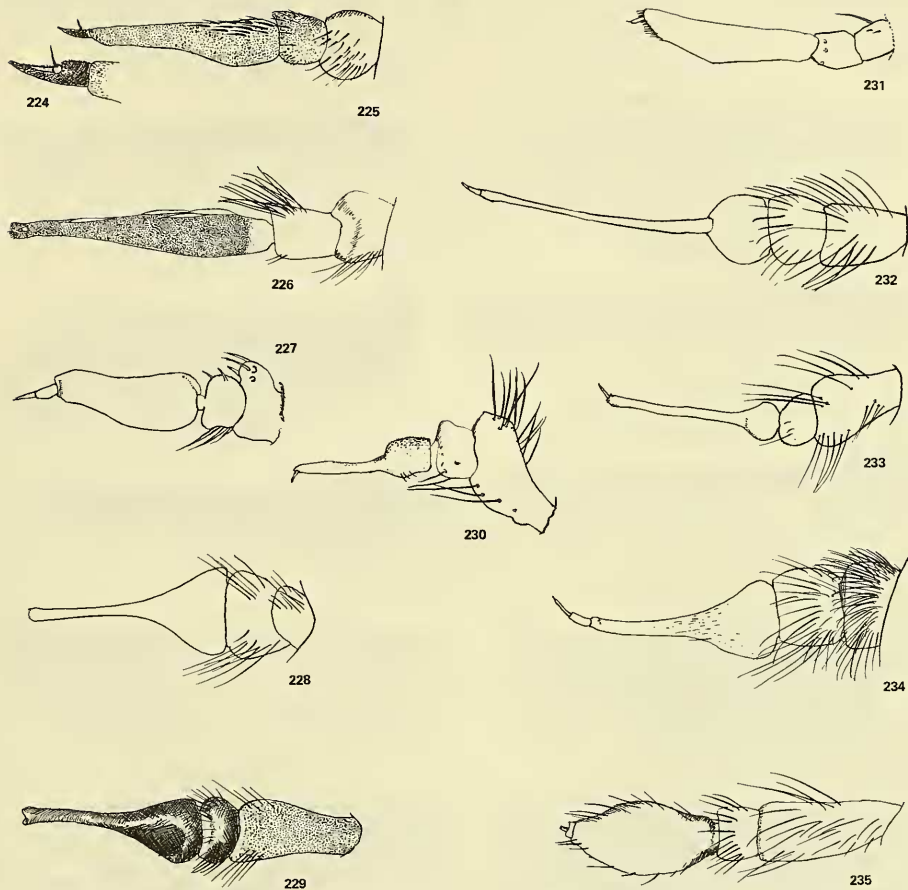
FIGURES 200-211.—200, *Stonyx* sp. 201, *Colossoptera latipennis* Brunnetti. 202, *Ligyra tenebrosa* Paramonov. 203, *Micomitra opalina* Hesse. 204, *Sparnopolius lherminieri* Macquart. 205, *Aphobantus* sp. 206, *Atrichochira pediformis* Bezzi.

207, *Bryodemina valida* Wiedemann. 108, *Exoprosopa minos* Meigen. 209, *Comptosia fascipennis* Macquart. 210, *Exoprosopa apicalis* Klug. 211, *Lepidanthrax* sp.



FIGURES 212-223.—212, *Sinaia kneuckeri* Becker, after Efflatoun. 213, *Aphobantus (Cononedys) erythraspis* Hermann, after Engel. 214, *Prothaplocnemis anthracina* Becker, after Engel. 215, *Phthiria pulicaria* Mikan, after Engel. 216, *Lomatia bella* Loew, after Engel. 217, *Thyridanthrax*

misellus Loew, after Engel. 218, *Thyridanthrax semifuscus* Engel, after Engel. 219, *Myonema* sp. 220, *Thyridanthrax vagans* Loew, after Engel. 221, *Thyridanthrax stigmulis* Klug, after Engel. 222, *Cyrtomorpha* sp. 223, *Adelogenys culicoides* Hesse.

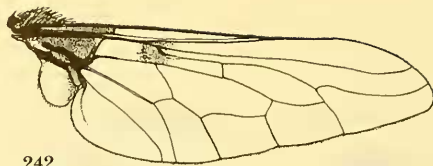


FIGURES 224–235.—224, *Nomalonia afra* Macquart, apex of antenna. 225, *Nomalonia afra* Macquart. 226, *Henica longirostris* Wiedemann. 227, *Aphobantus claripennis* Becker, after Engel. 228, *Chionamoeba choreutes* Bowden, paratype. 229, *Synthesia fucoides* Bezzi. 230, *Oestranthrax kara-*

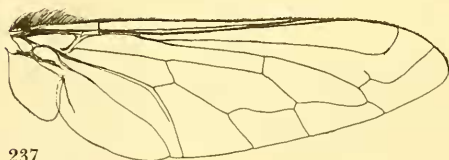
vajevi Paramonov, after Engel. 231, *Oligodranes flavus* Paramonov, after Engel. 232, *Rhynchanthrax parvicornis* Loew. 233, *Oestranthrax brunescens* Loew, after Engel. 234, *Petrorossia phthinoxantha* Hesse. 235, *Sphenoidoptera varipennis* Williston.



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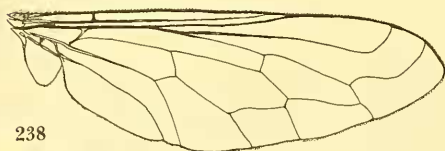
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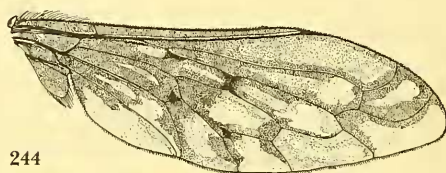
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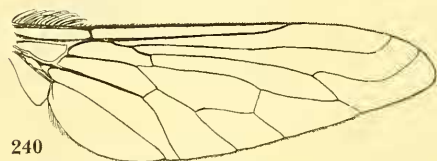
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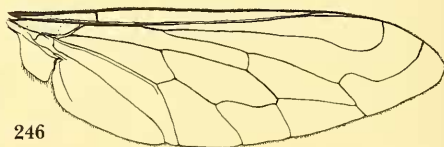
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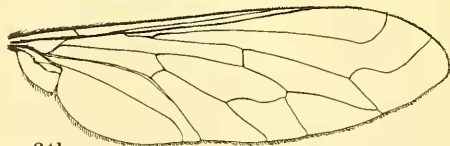
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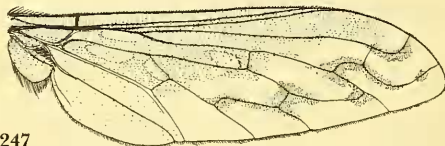
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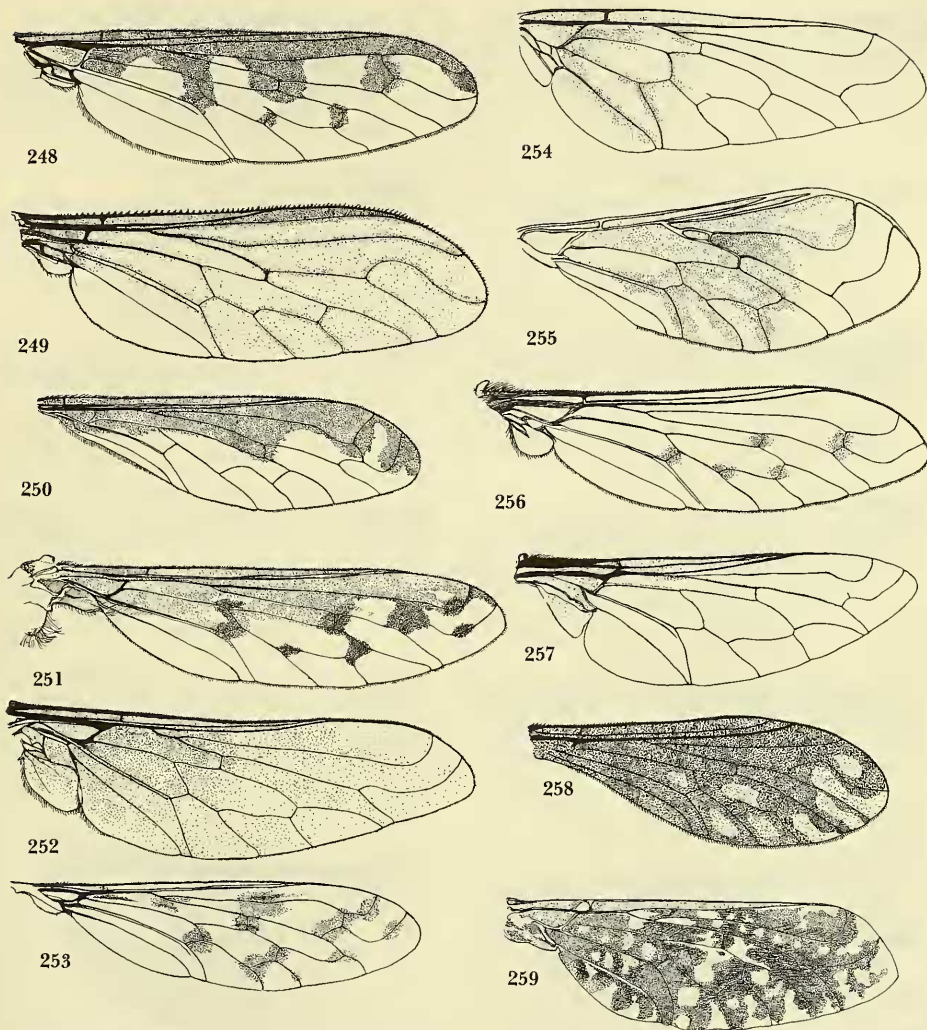
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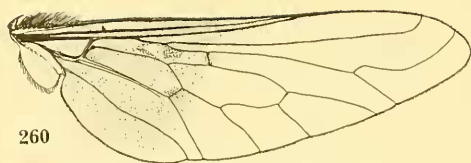
FIGURES 236-247.—236, *Systoechus vulgaris* Osten Sacken. 237, *Acanthogeron senex* Wiedemann. 238, *Lissomerus niveicomatus* Austen, holotype. 239, *Anastoechus trisignatus* Portschinsky, female. 240, *Anastoechus nitidulus* Fabricius. 241, *Sisyrophanus pyrrocerus* Bezzi, type. 242, *Zinnomyia*

karooensis Hesse, paratype. 243, *Sisyrophanus abdominalis* Bezzi, type. 244, *Bombylius (Triplasius)* sp., Atlas Mts. 245, *Bombylius major* Linné. 246, *Isocnemus nemestrinus* Bezzi, type. 247, *Bombylius (Triplasius) bivittatus* Loew.



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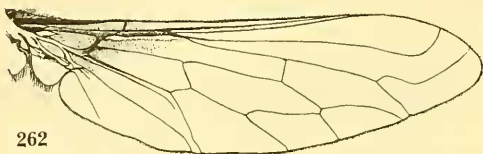
Legnotomyia cinerea Austen, type. 255, *Legnotomyia trichorhoa* Loew. 256, *Adelidea anomala* Wiedemann. 257, *Eusurbus nigrocinctus* Roberts. 258, *Eclimus gracilis* Loew. 259, *Proracthes longirostris* Bezzi.



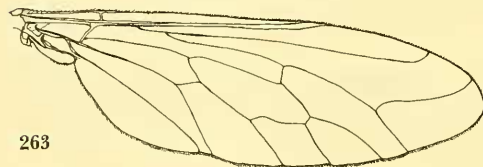
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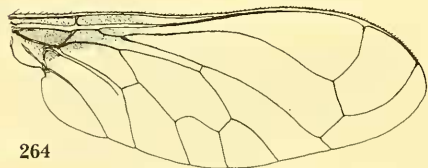
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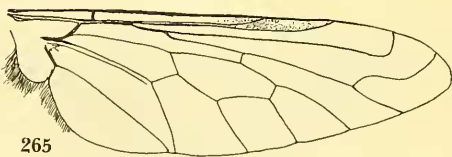
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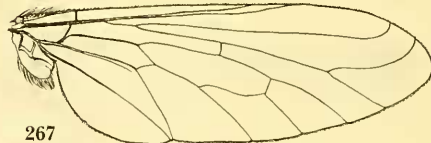
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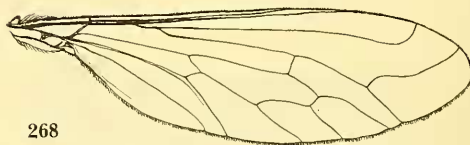
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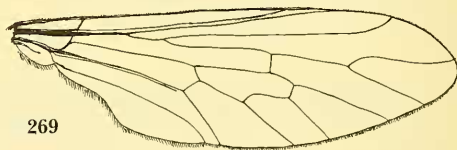
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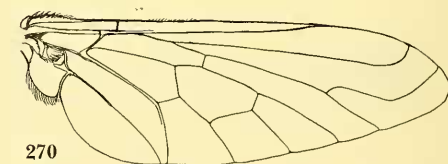
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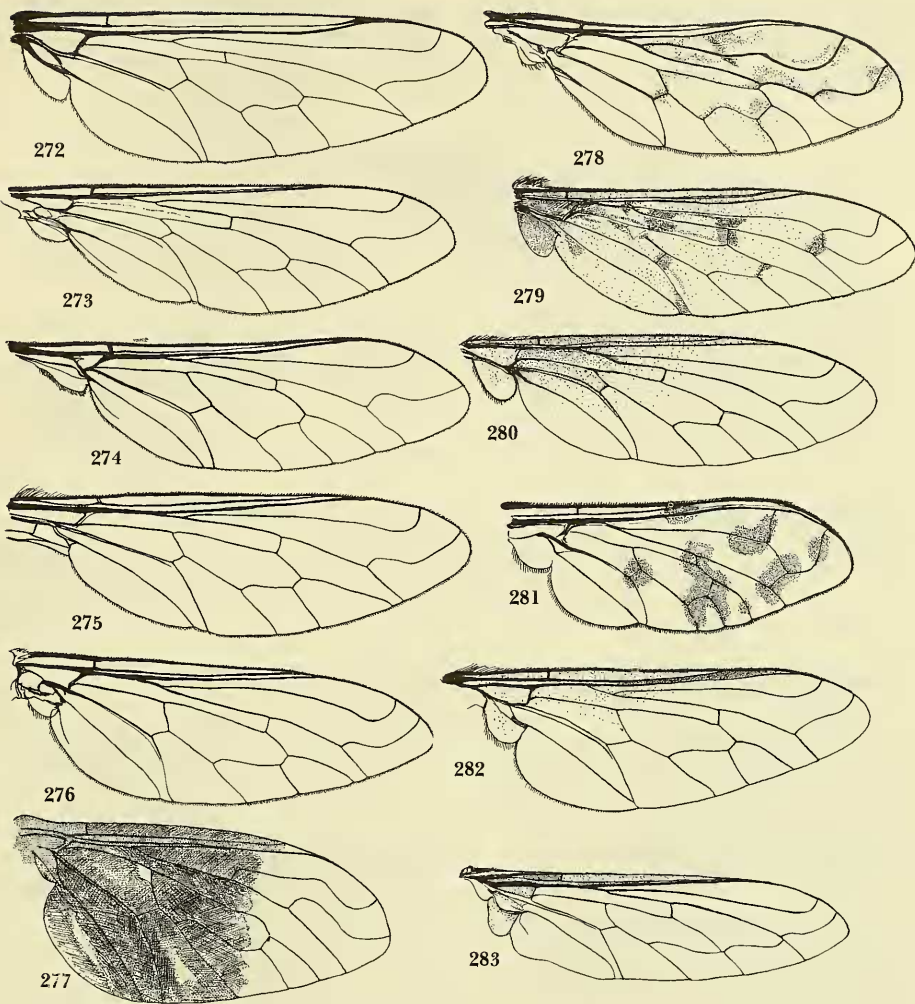
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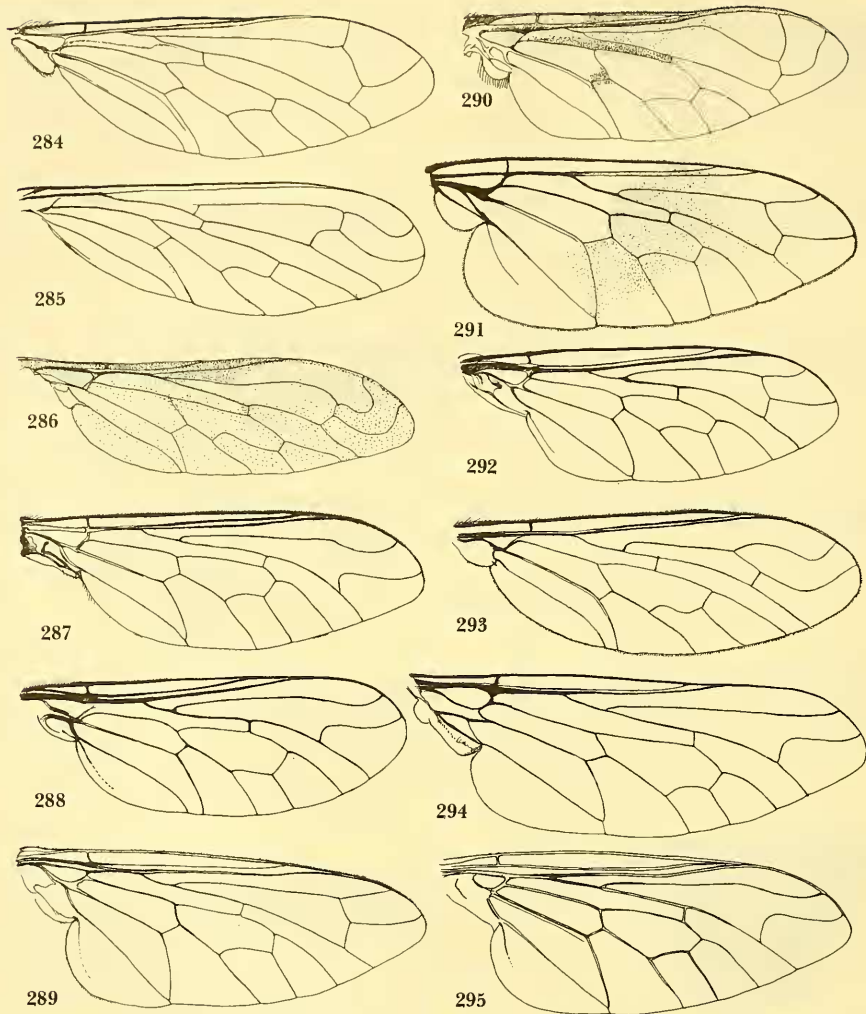
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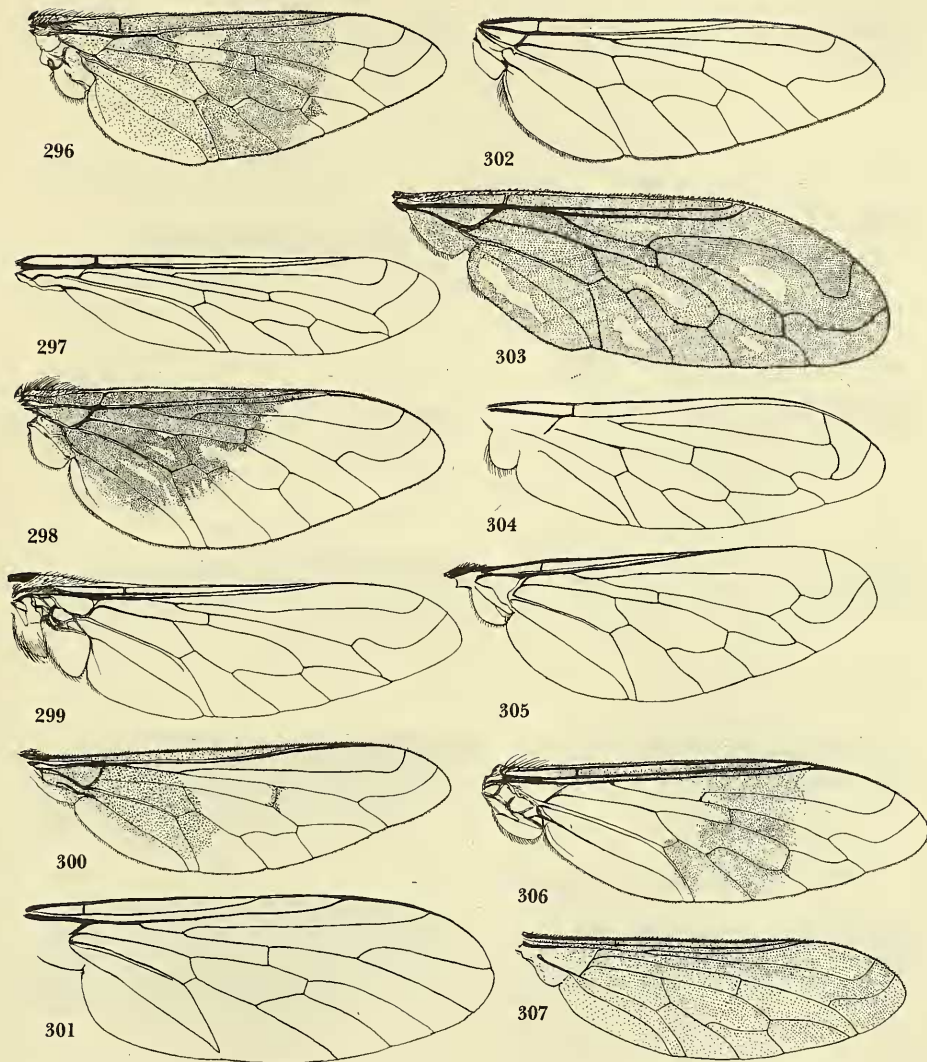
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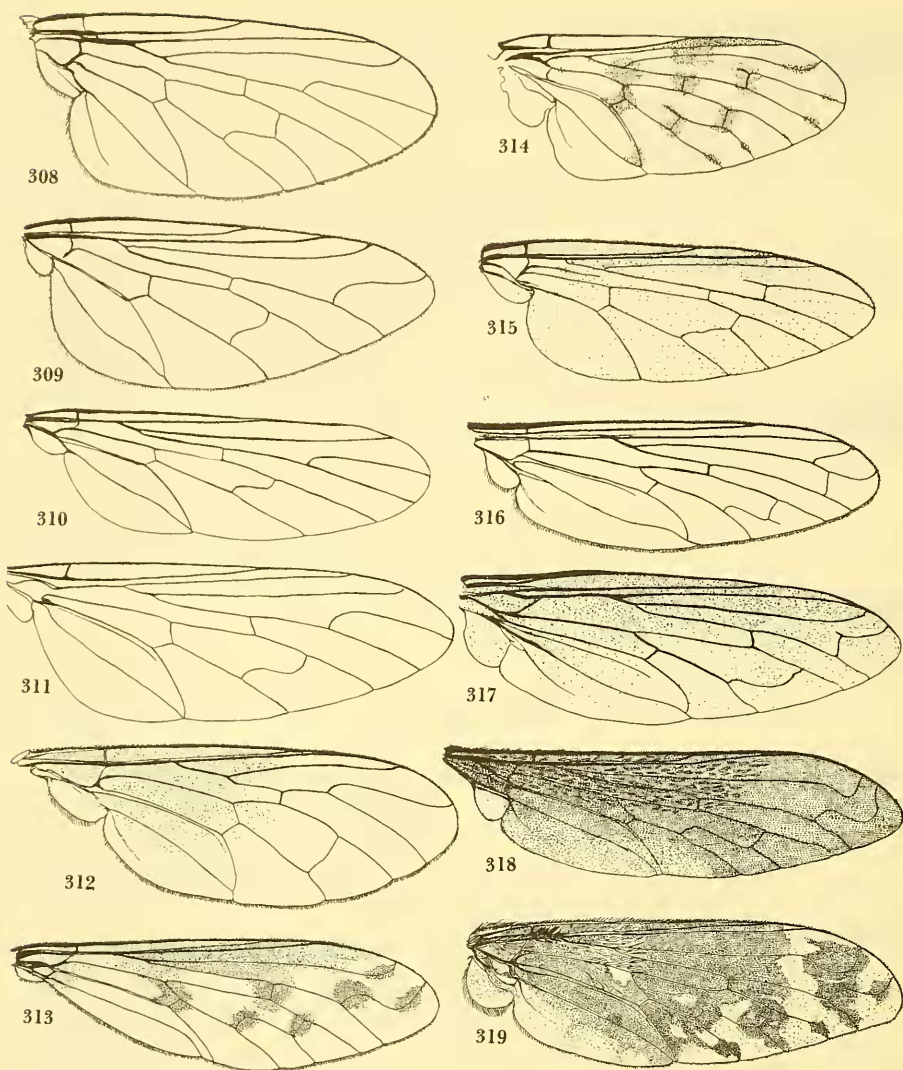
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290, *Lordotus gibbus* Loew. 291, *Mariobezzia griseohirta* Nurse. 292, *Callynthrophora capensis* Schiner. 293, *Exepacmus johnsoni* Coquillett. 294, *Zyxmyia megachile* Bowden, after Bowden. 295, *Hyperusia luteifacies* Bezzi, type.



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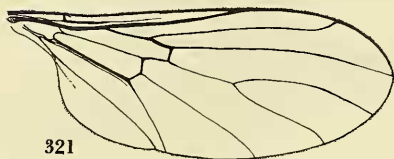
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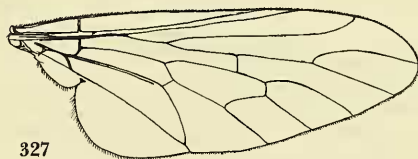
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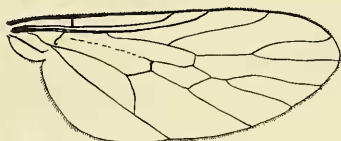
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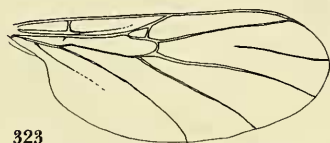
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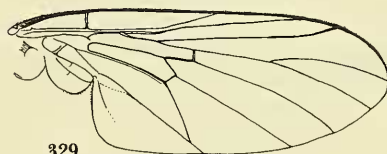
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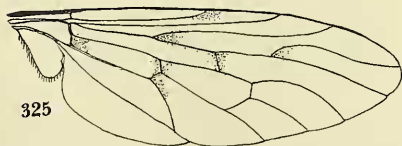
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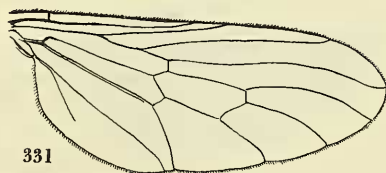
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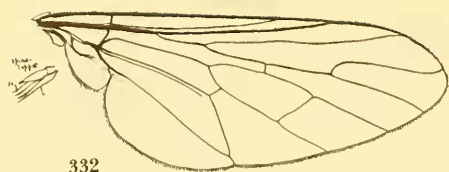
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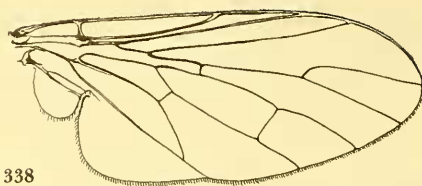
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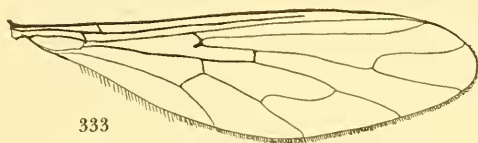
327, *Crocidium melanopalís* Hesse, paratype. 328, *Empidideicus turneri* Hesse, paratype. 329, *Apolysis maherniaphila* Hesse, paratype. 330, *Cyrtisiopsis crassirostris* Hesse, paratype. 331, *Platypygus melleus* Bezzi, after Eflattoun.



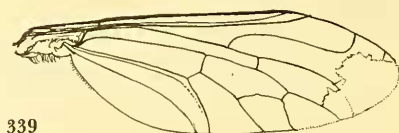
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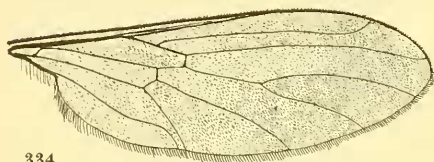
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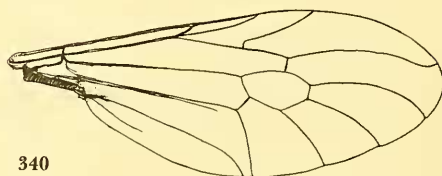
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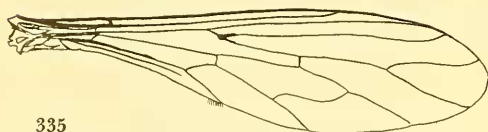
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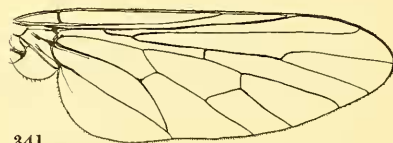
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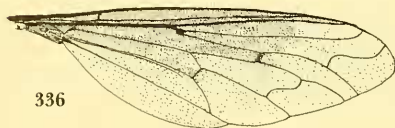
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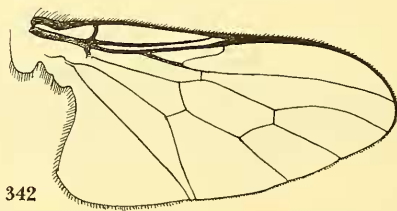
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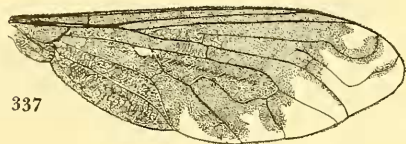
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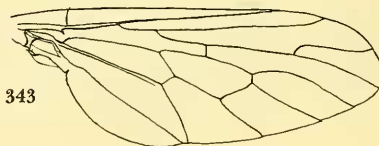
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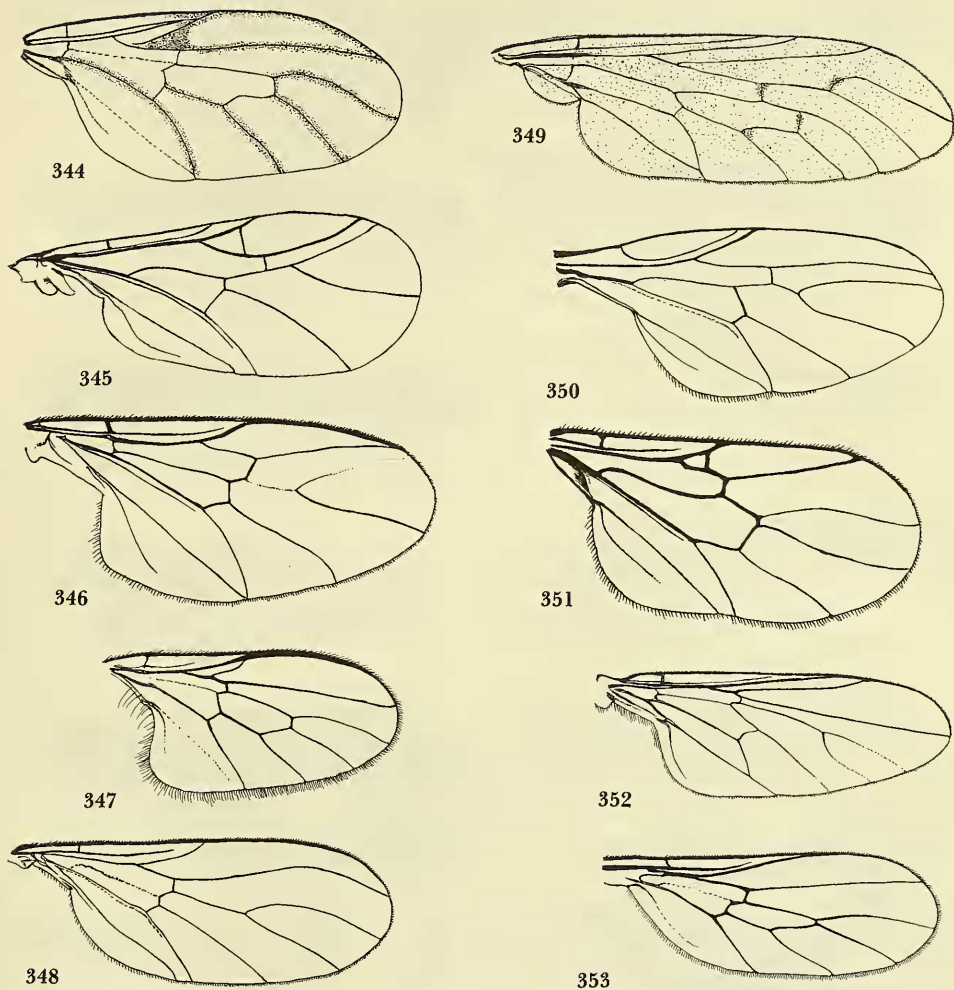
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345, *Pseudoglabellula meridionalis* Hesse, after

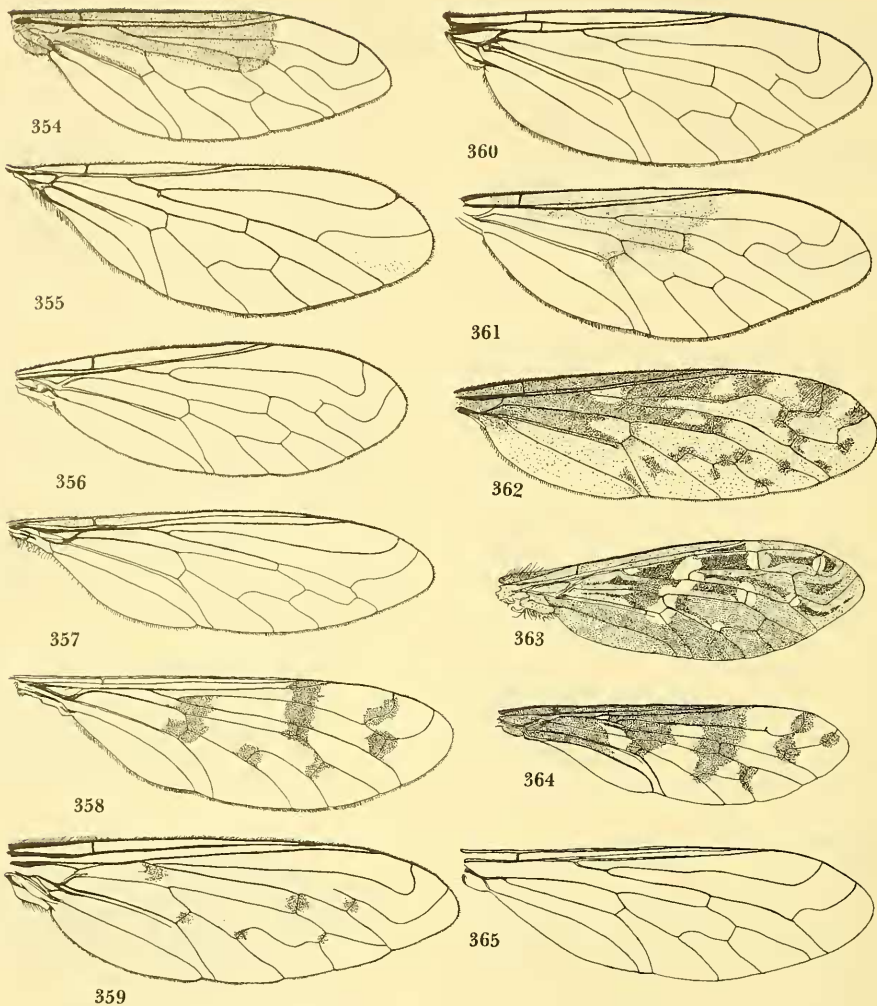
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Eflatoun. 347, *Mythicomyia pusillima* Edwards,

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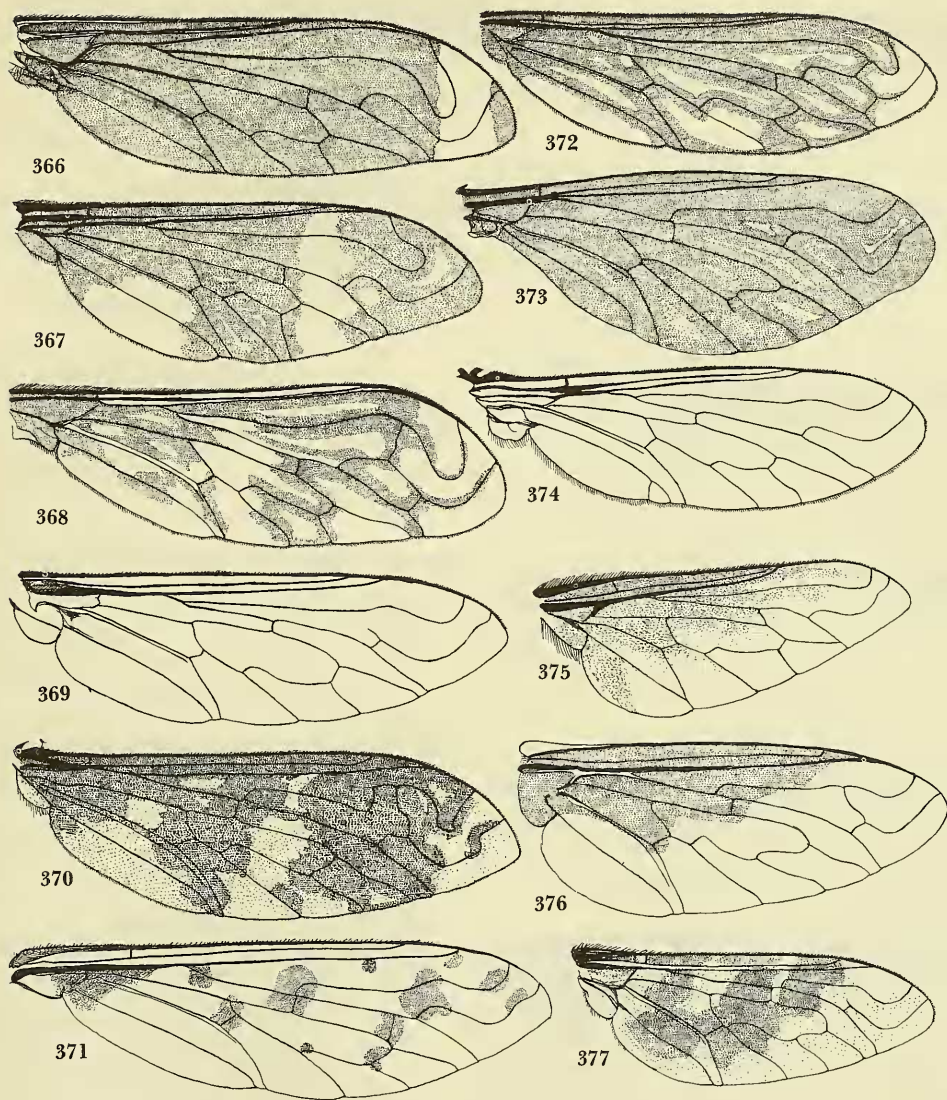
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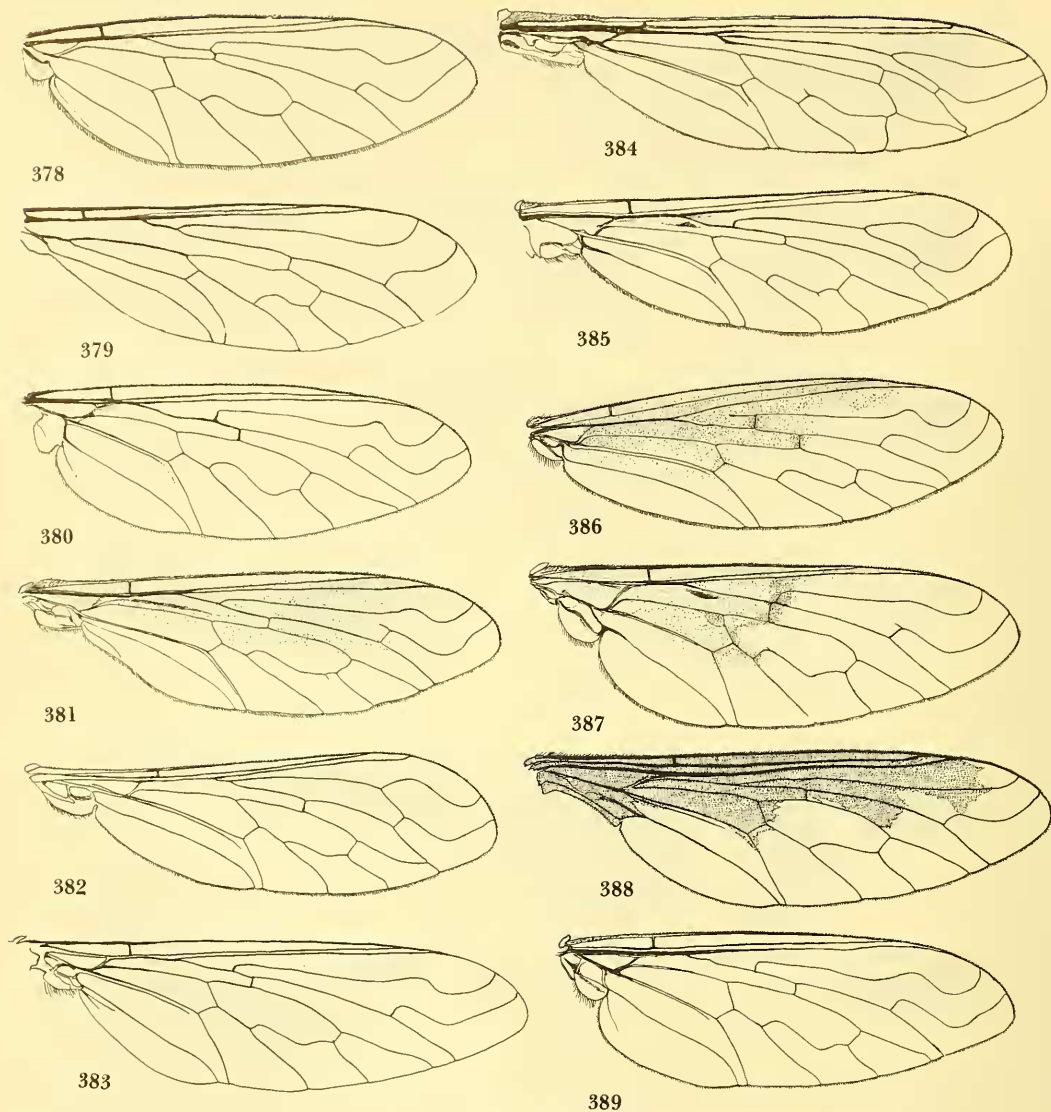
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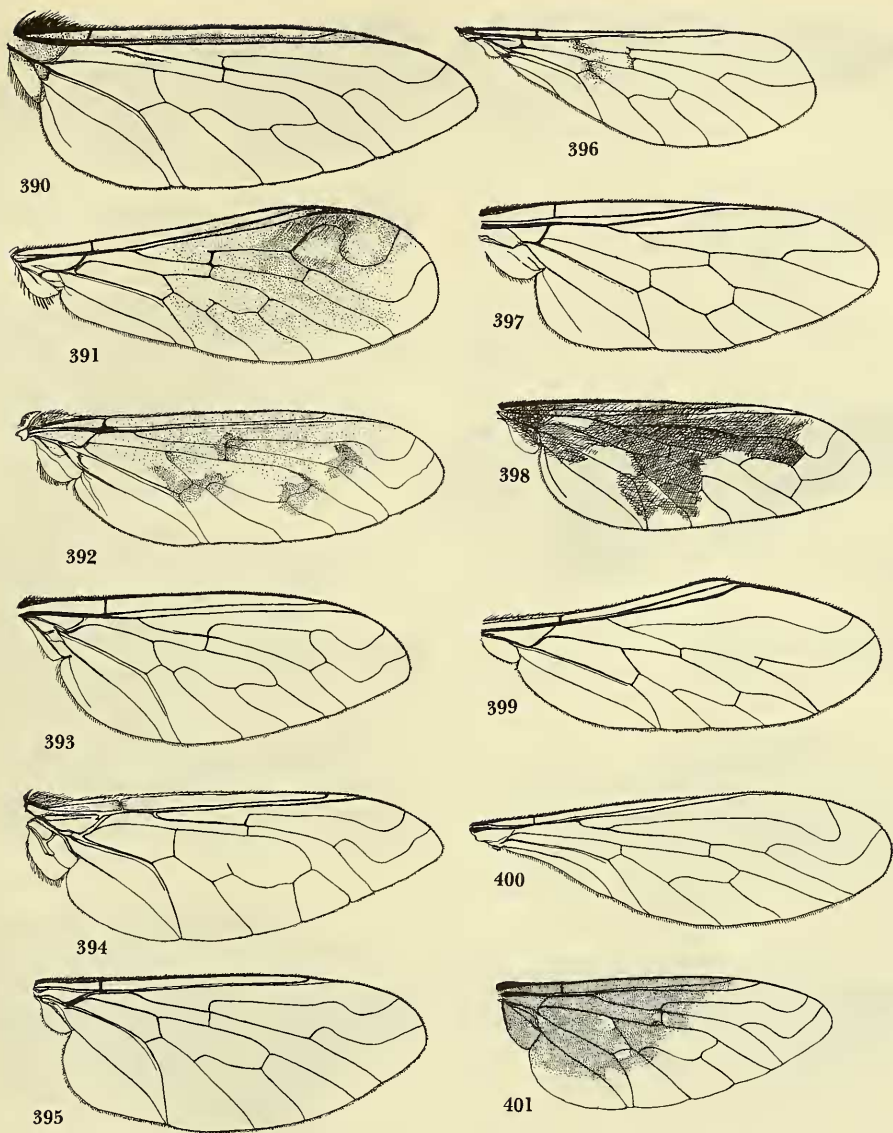
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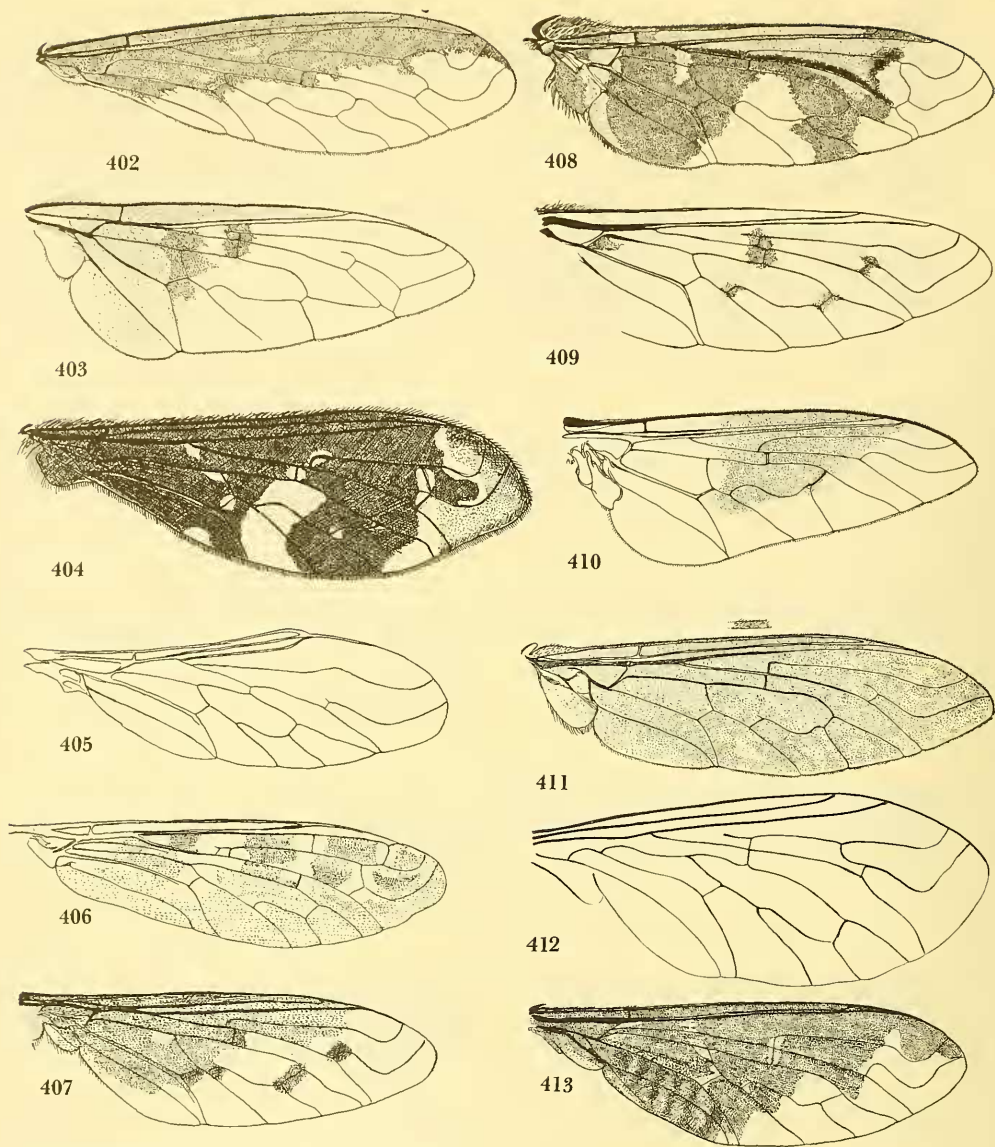
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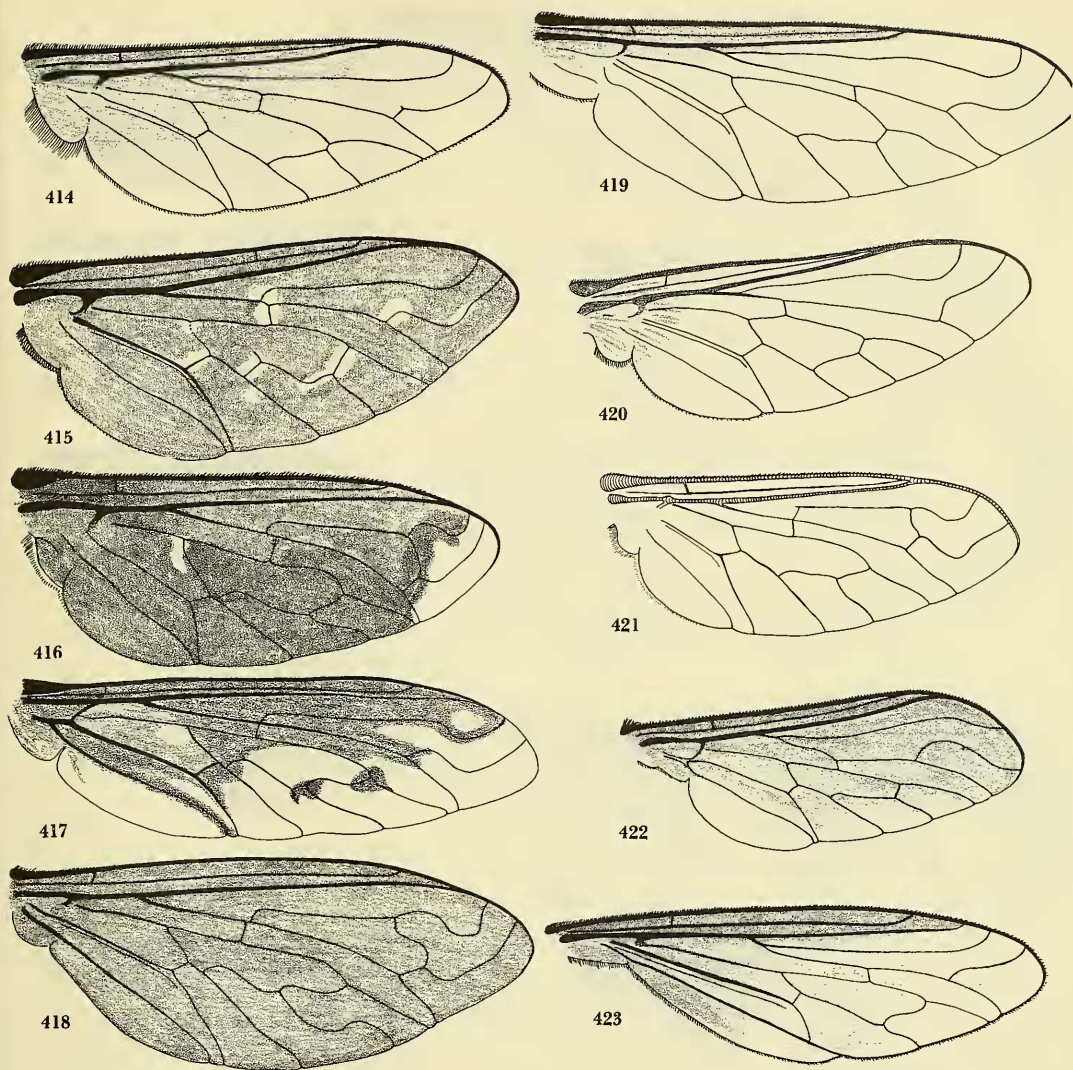
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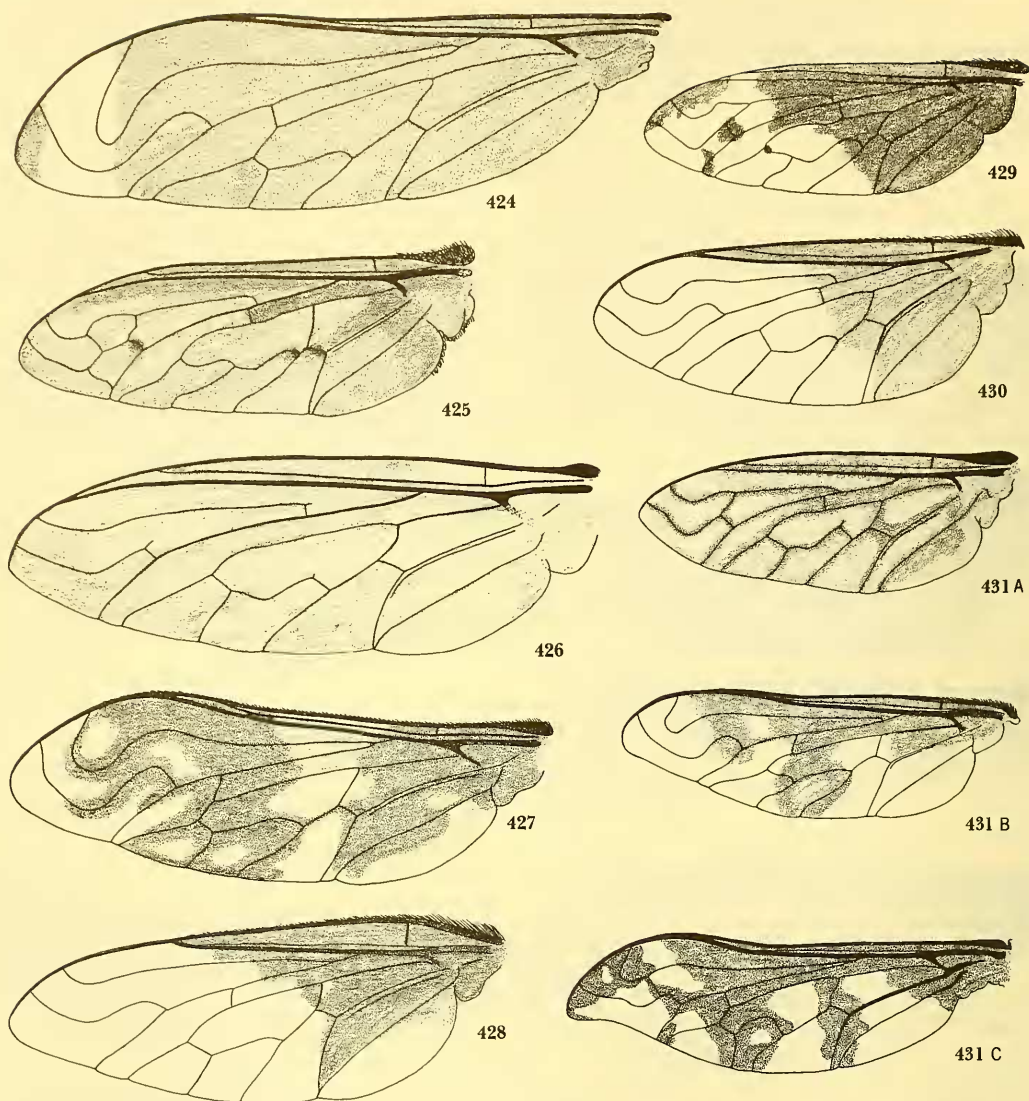
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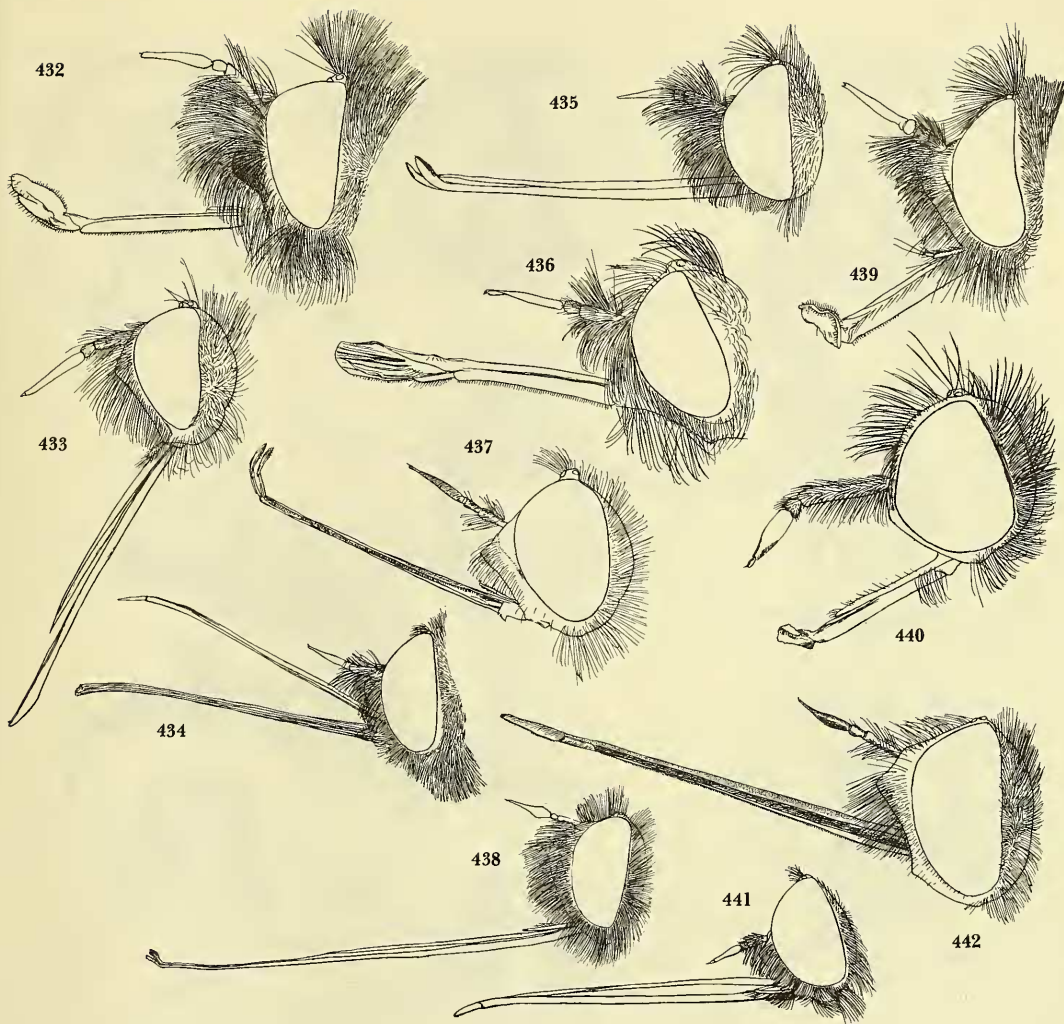
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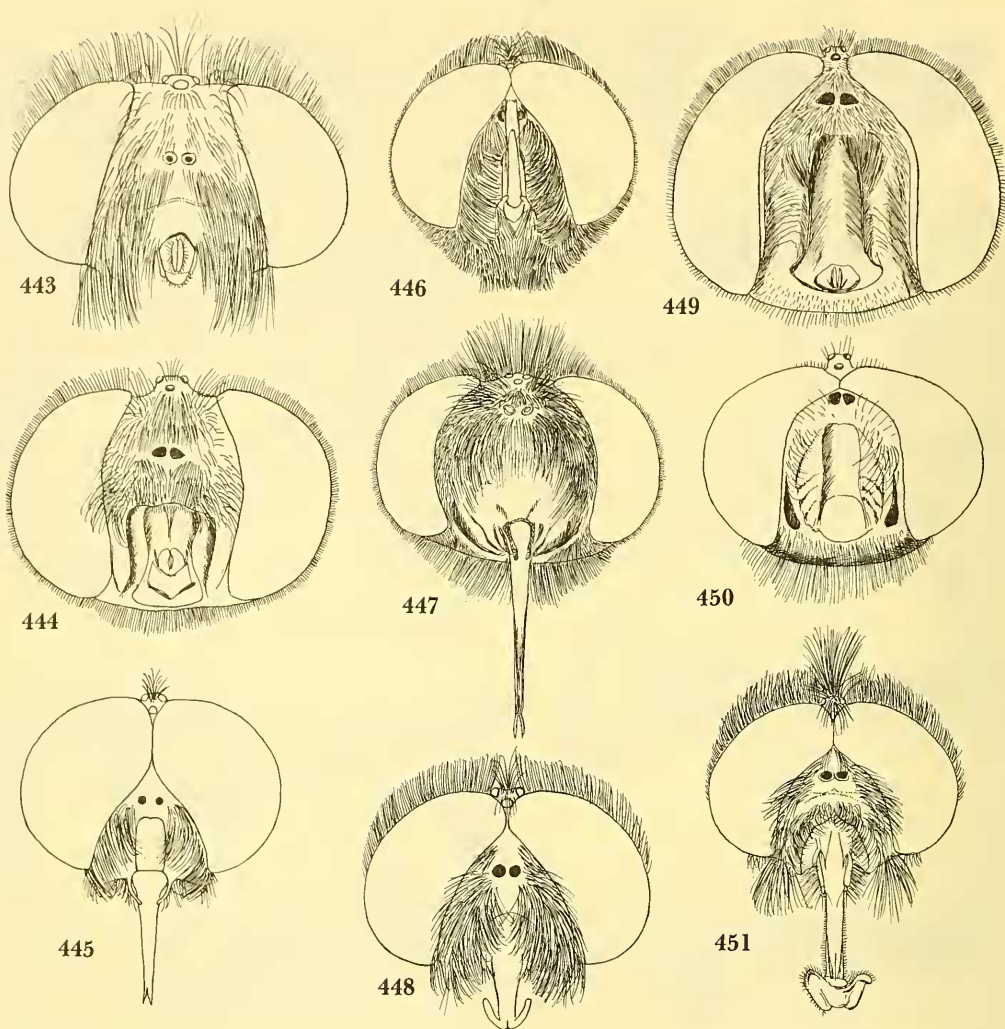
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429, *Stonyx clotho* Wiedemann. 430, *Syntheria fucoides* Bezzi. 431A, *Atrichochira pediformis* Bezzi. 431B, *Doddosia picta* Edwards. 431C, *Ulosometa falcata*, new species.



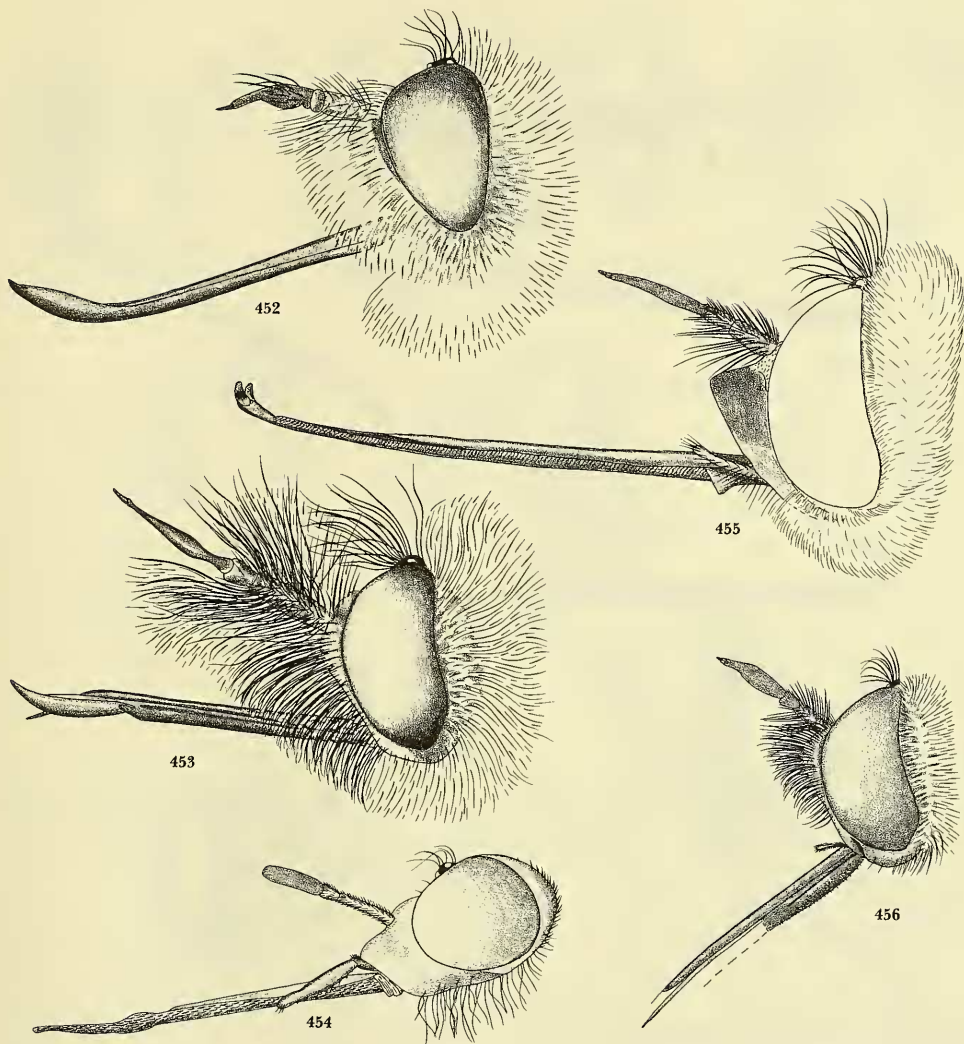
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sphenoptera Loew. 438, *Bombylodes eximius* Becker. 439, *Eusurbus crassilabris* Macquart. 440, *Tillyardomyia gracilis* Tonnoir. 441, *Isochnemus nemestrinus* Bezzi, from type. 442, *Systoechus vulgaris* Loew.



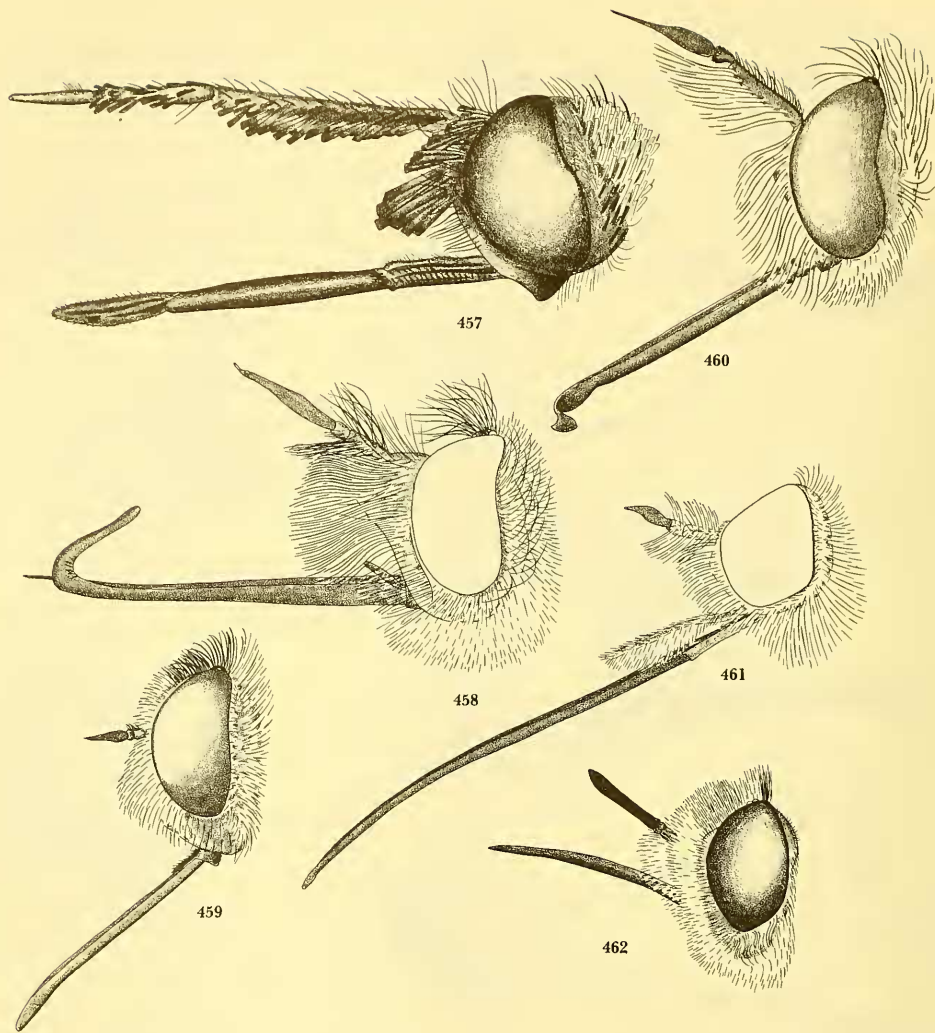
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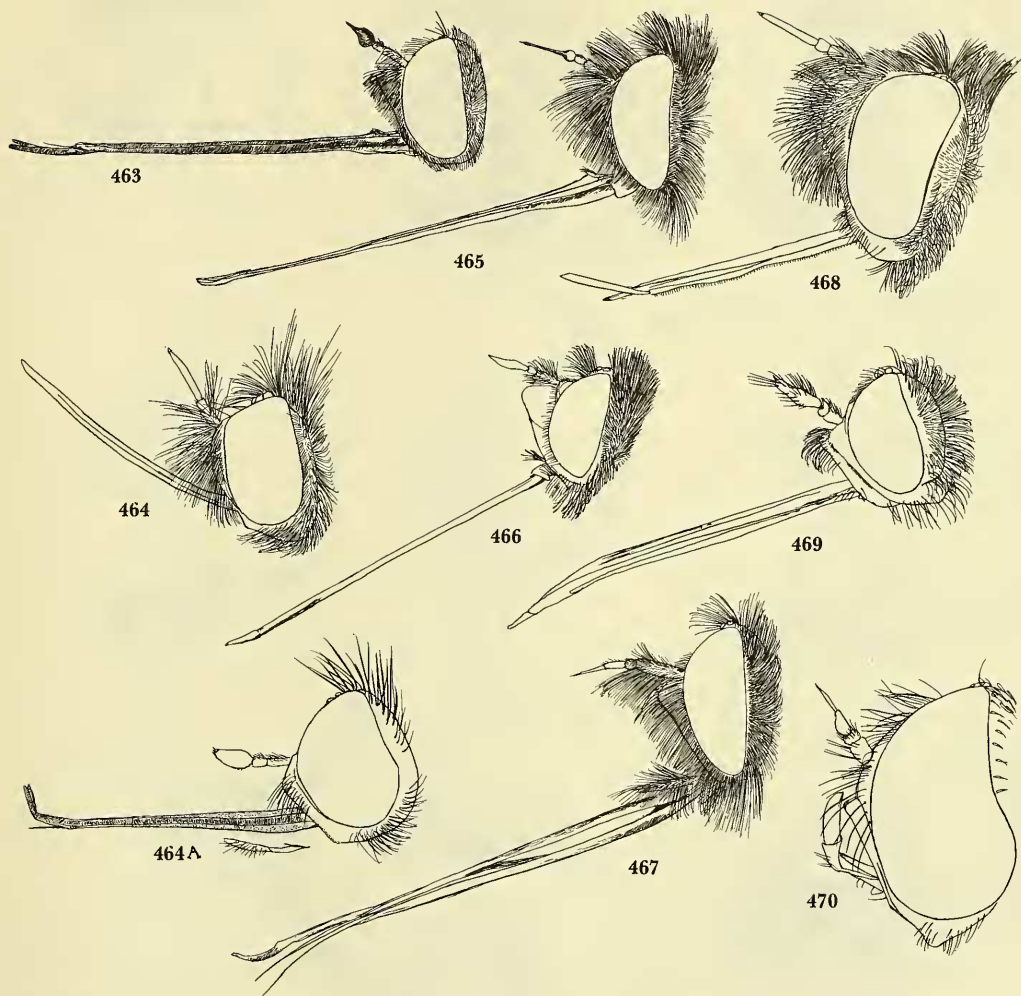
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453, *Dischistus mystax* Wiedemann. 454, *Eclimus*

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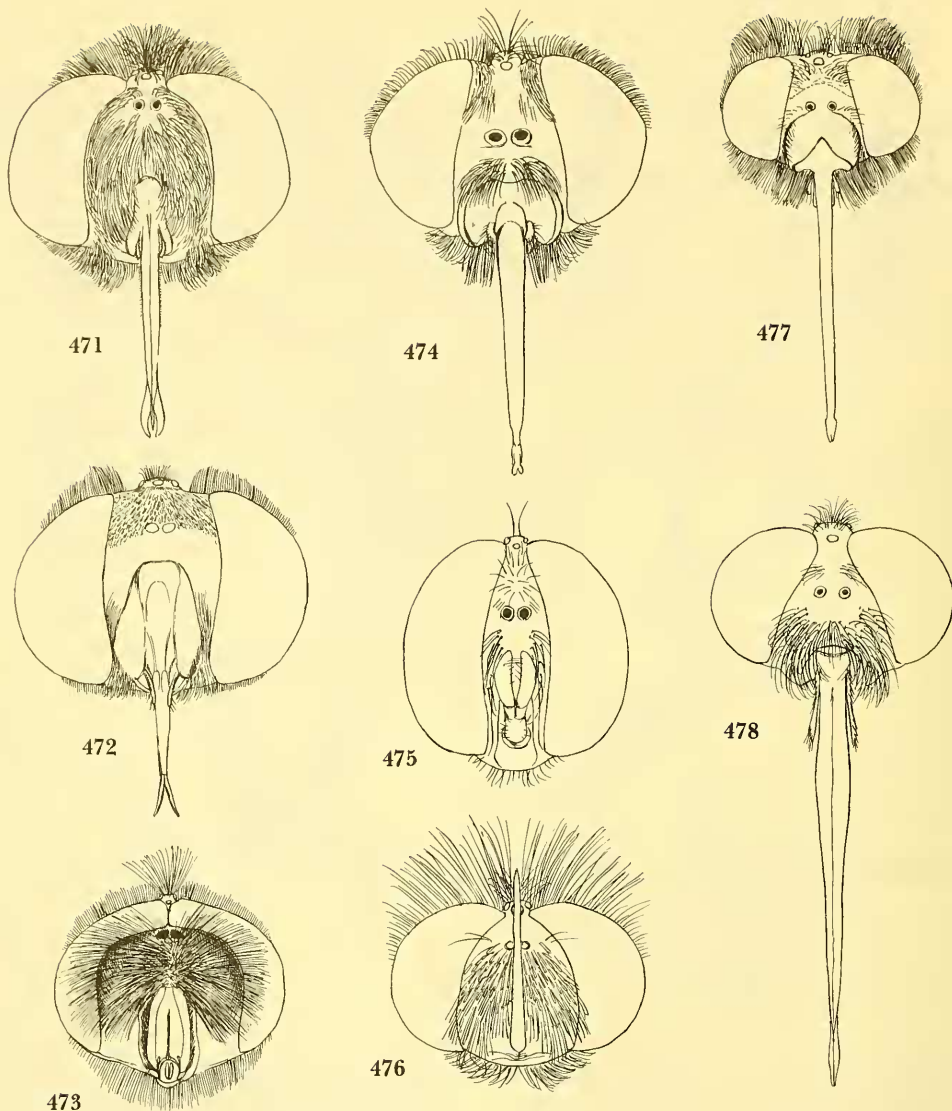
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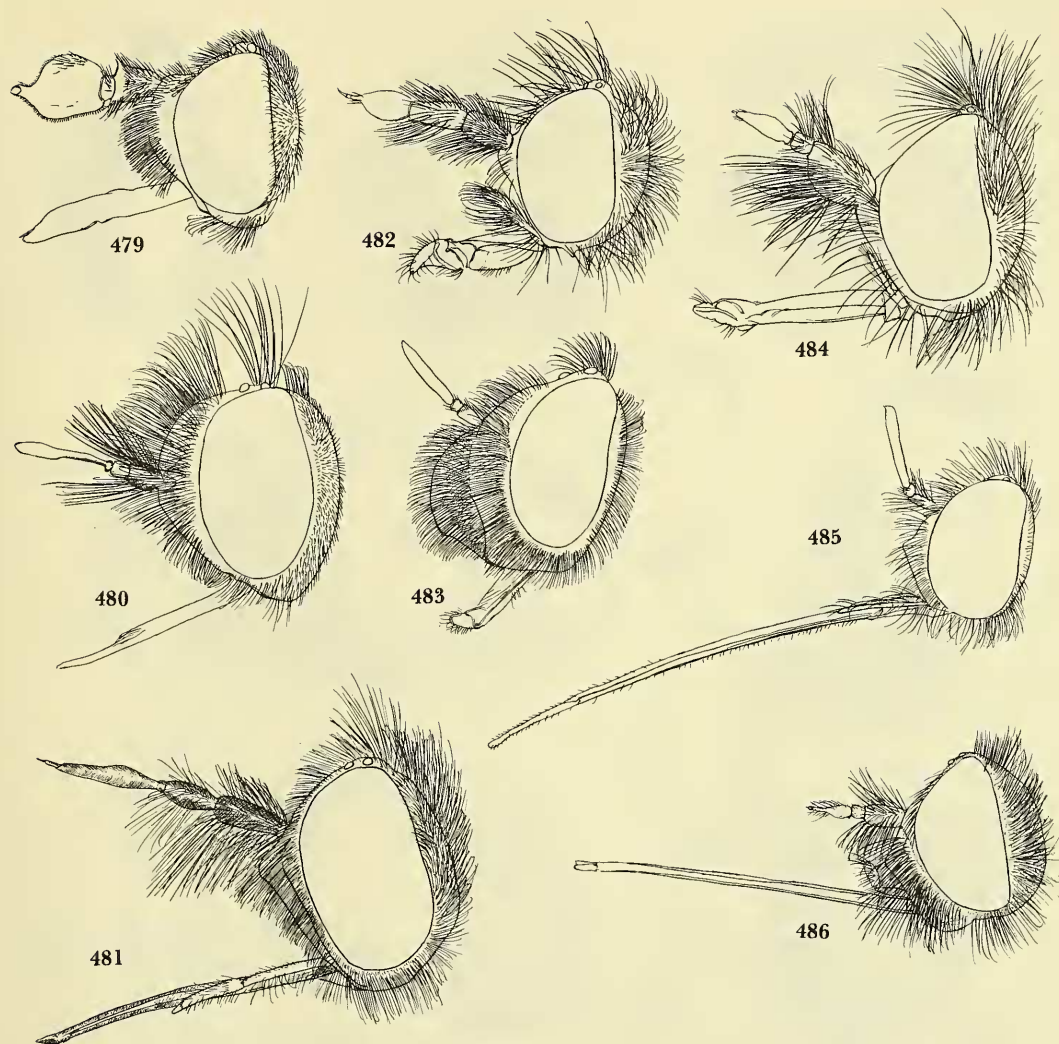
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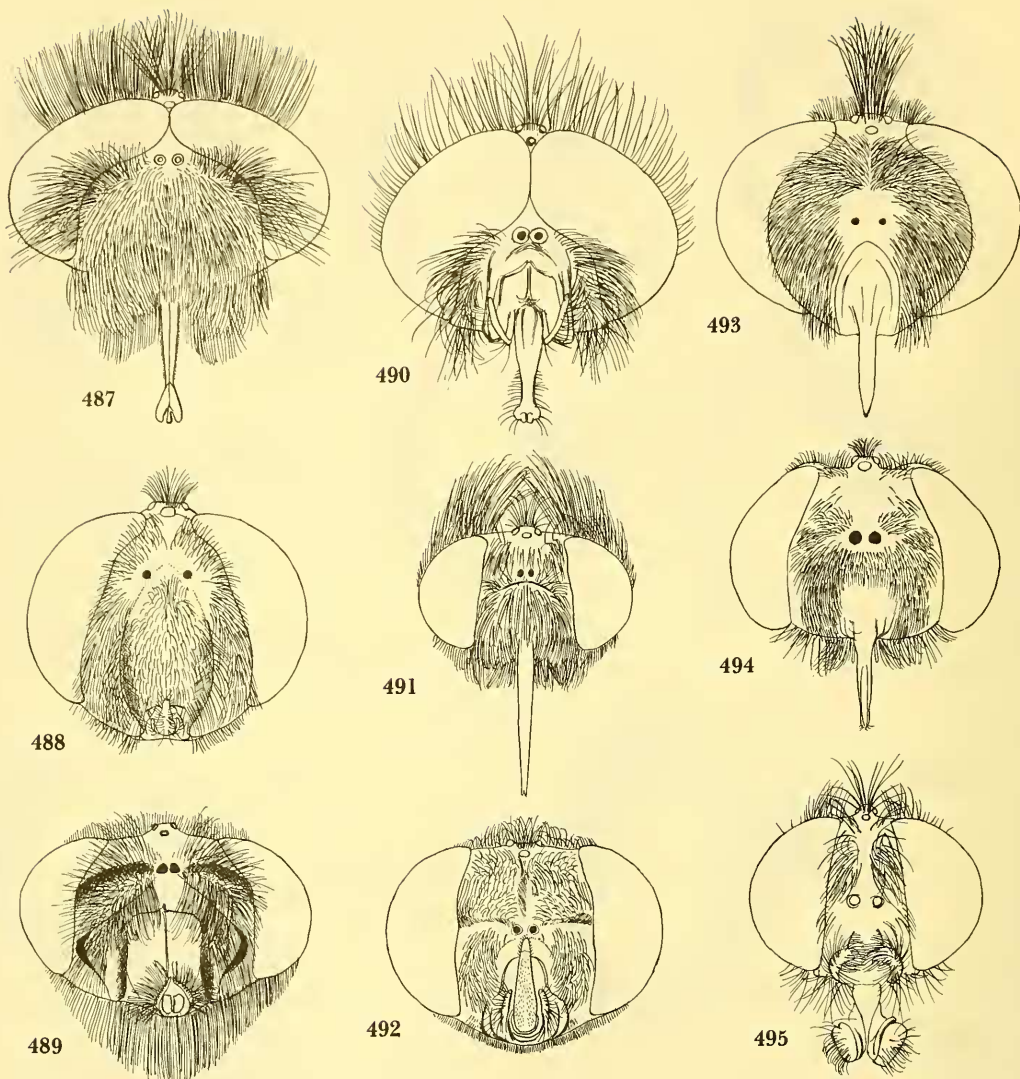
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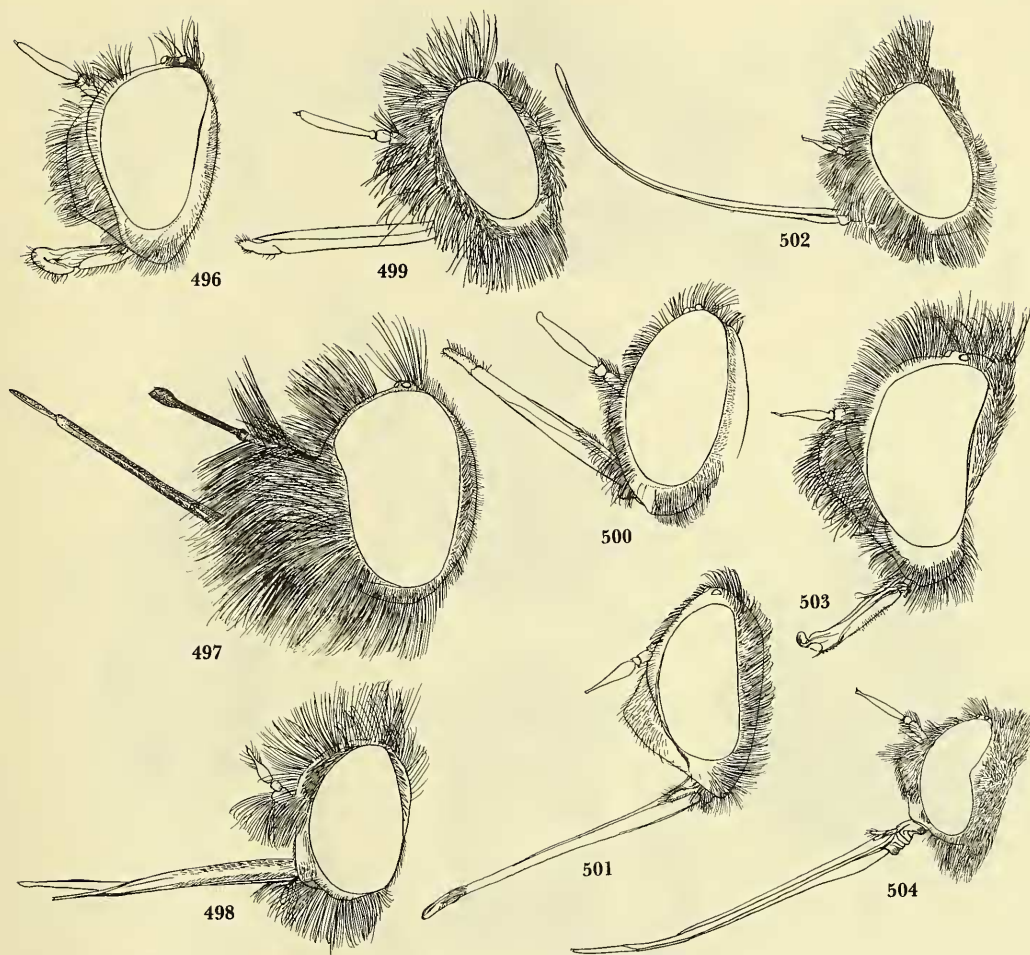
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Bezzi. 484, *Conophorus fuliginosus*. 485, *Megapalpus capensis* Wiedemann. 486, *Platamomyia depressus* Loew.



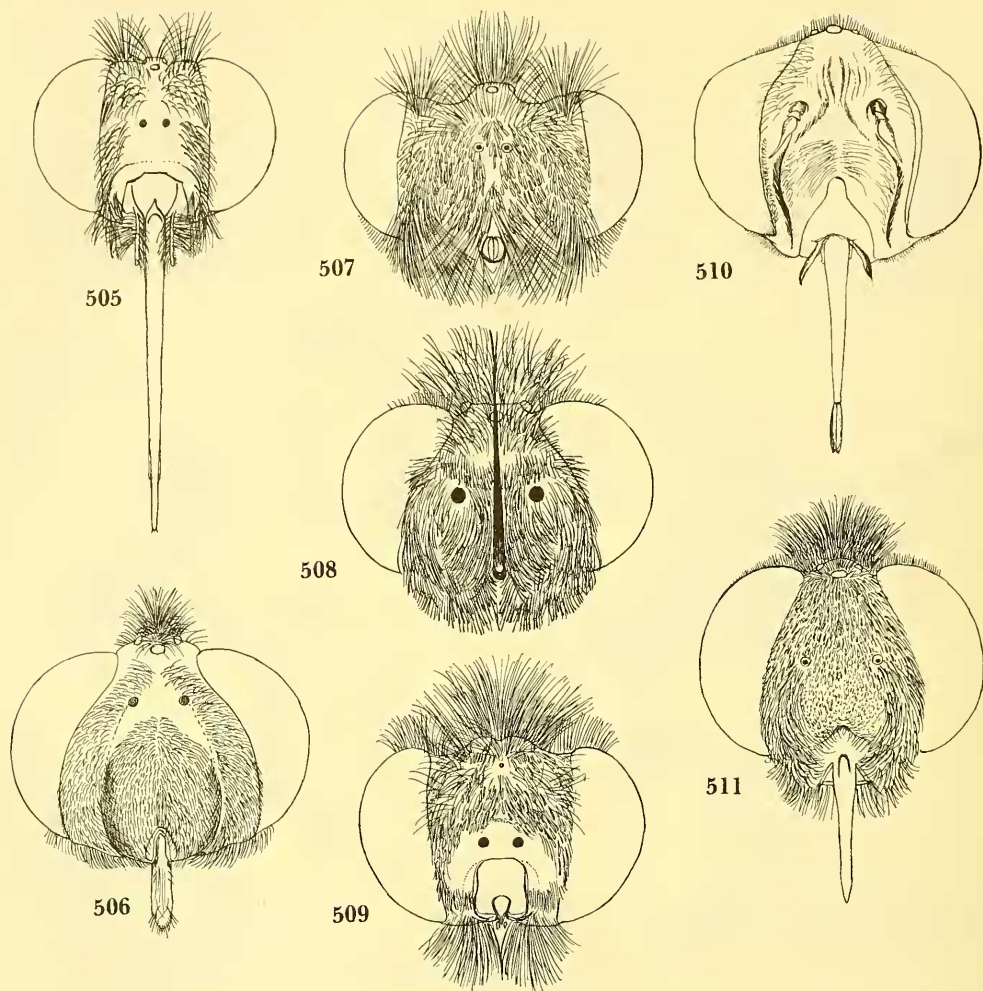
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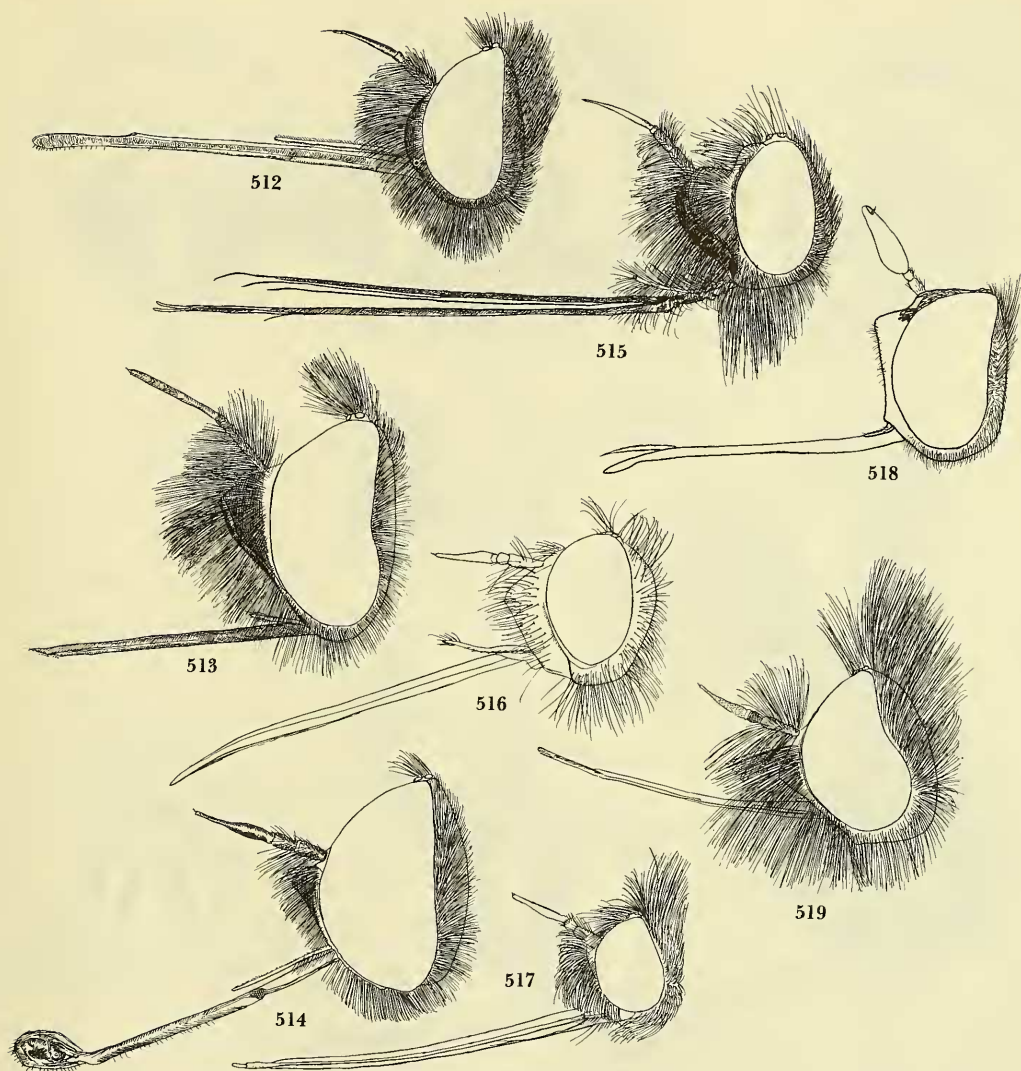
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luteifacies Bezzi. 501, *Gyrocraspedum pleskei* Becker. 502, *Sericosoma squamiventris* Edwards, type. 503, *Cytherea (Chalcochiton) pallasii* Loew. 504, *Heterostylum robustum* Osten Sacken.



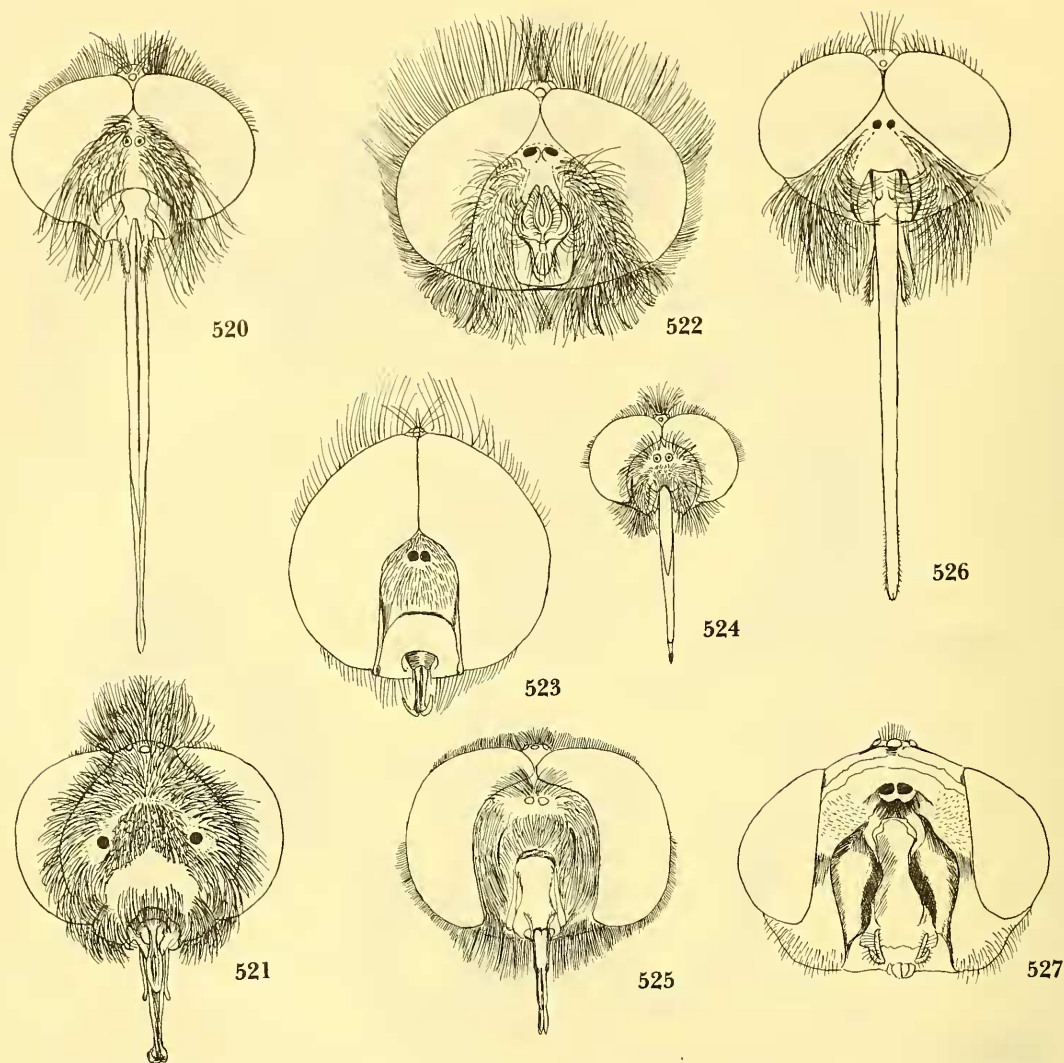
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romyia pachyceratus Bigot. 510, *Gyrocraspedum pleskei* Becker. 511, *Callostoma fascipenne palaestinae* Paramonov.



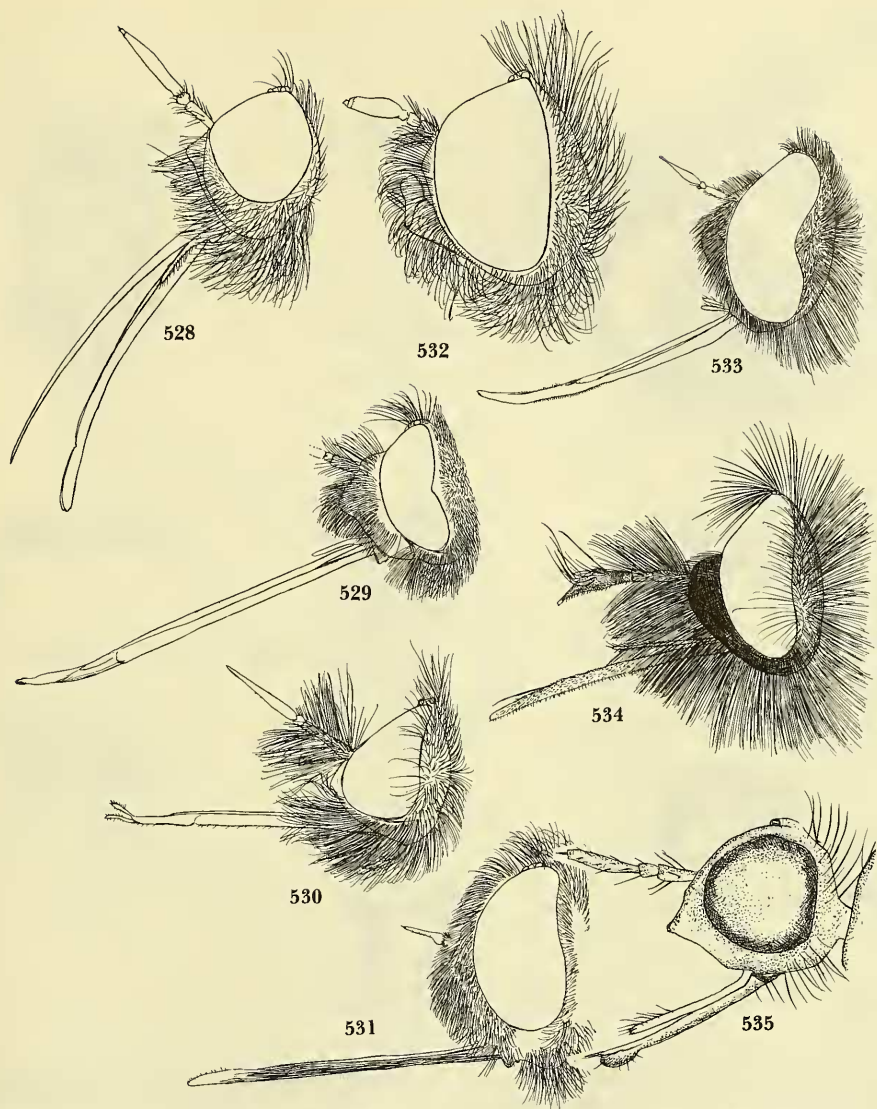
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Hesse, paratype. 517, *Sericusia lanata* Edwards, type. 518, *Neodischistus collaris* Painter, type. 519, *Hallidia plumipilosa* Hull, from type.



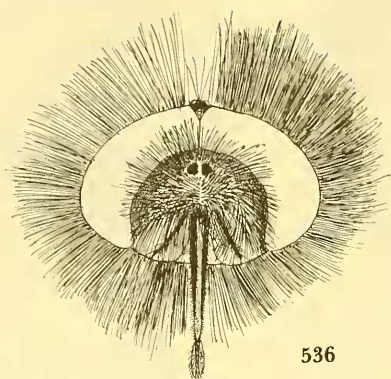
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neurus Macquart. 525, *Eurycarenum laticeps* Loew. 526, *Crocidium melanopalis* Hesse. 527, *Heterotropus aegyptiacus* Paramonov.

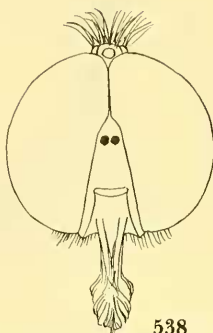


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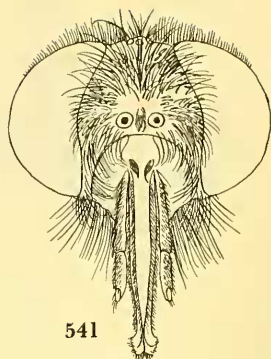
phthiria lanata Edwards, holotype. 533, *Eurycarenus laticeps* Loew. 534, *Acreotrichus gibbicornis* Macquart. 535, *Semiramis punctipennis* Becker, after Becker.



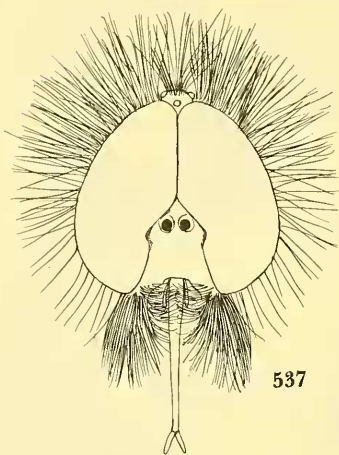
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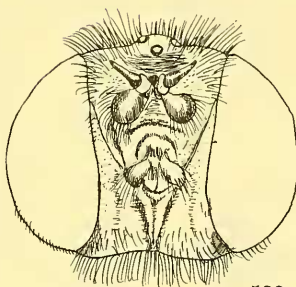
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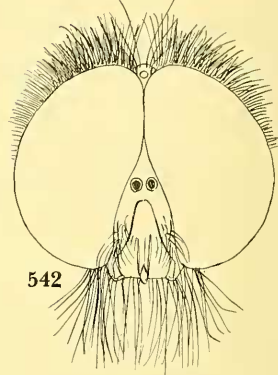
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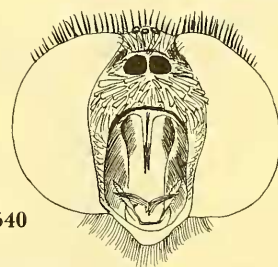
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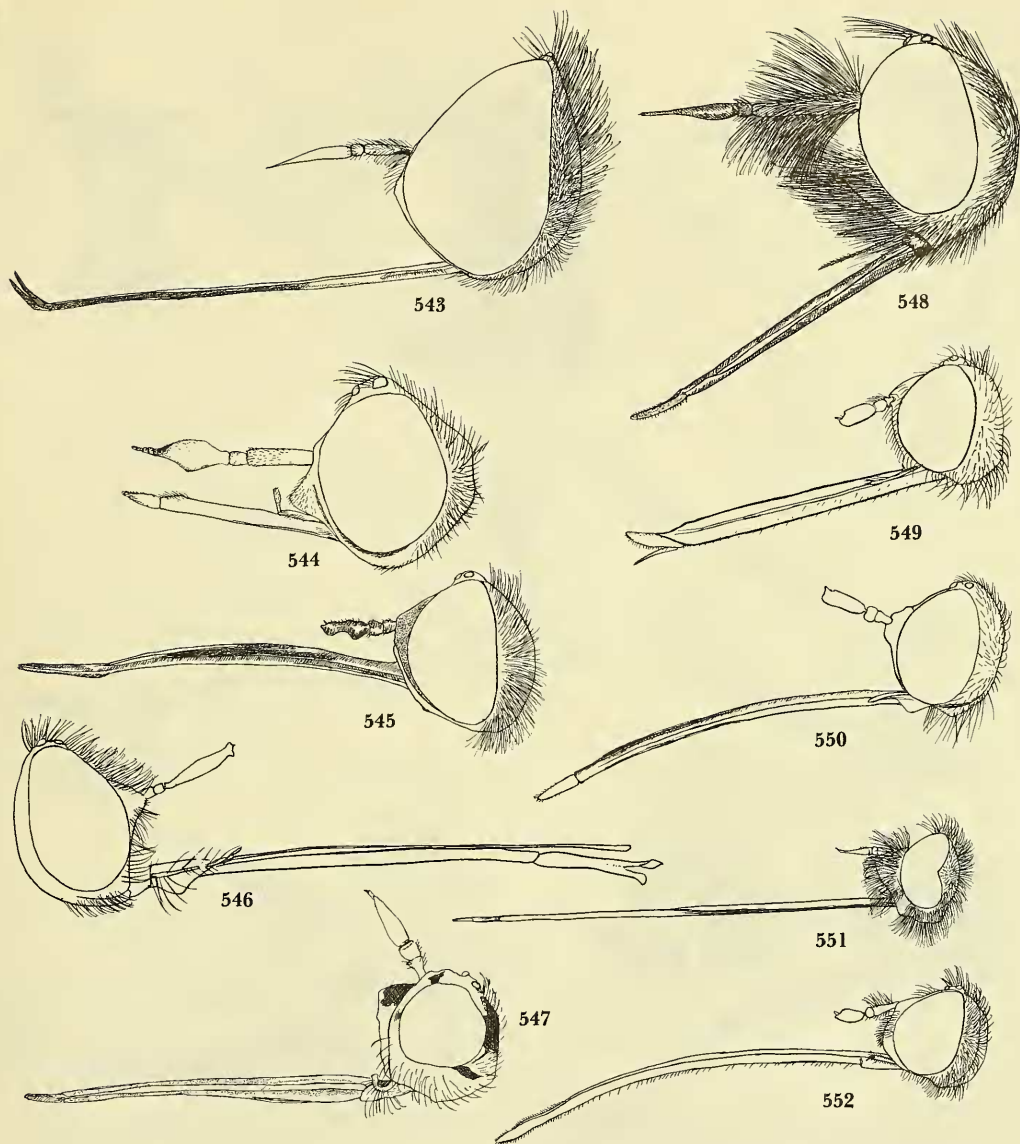
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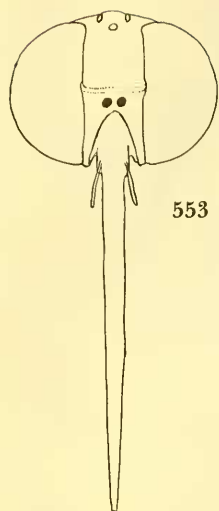
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540, *Lepidophora lepidocera* Wiedemann. 541, *Cyrtomyia chilensis* Paramonov. 542, *Marmasoma sumptuosa* White.

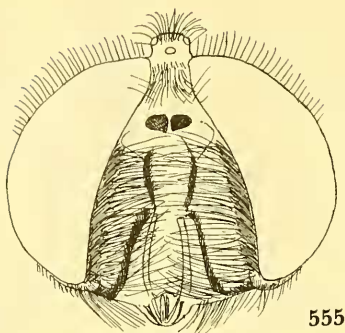


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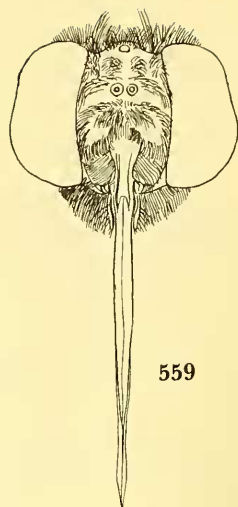
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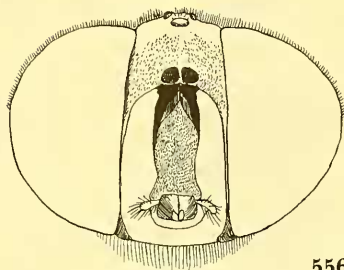
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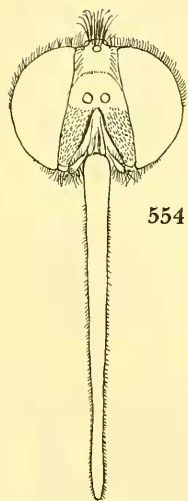
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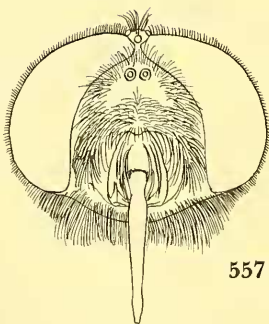
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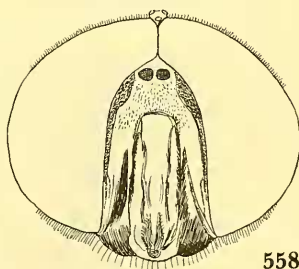
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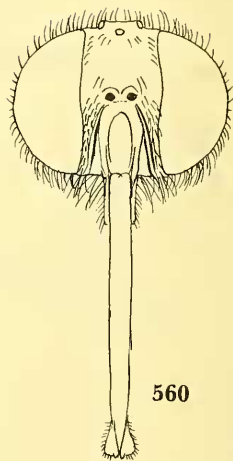
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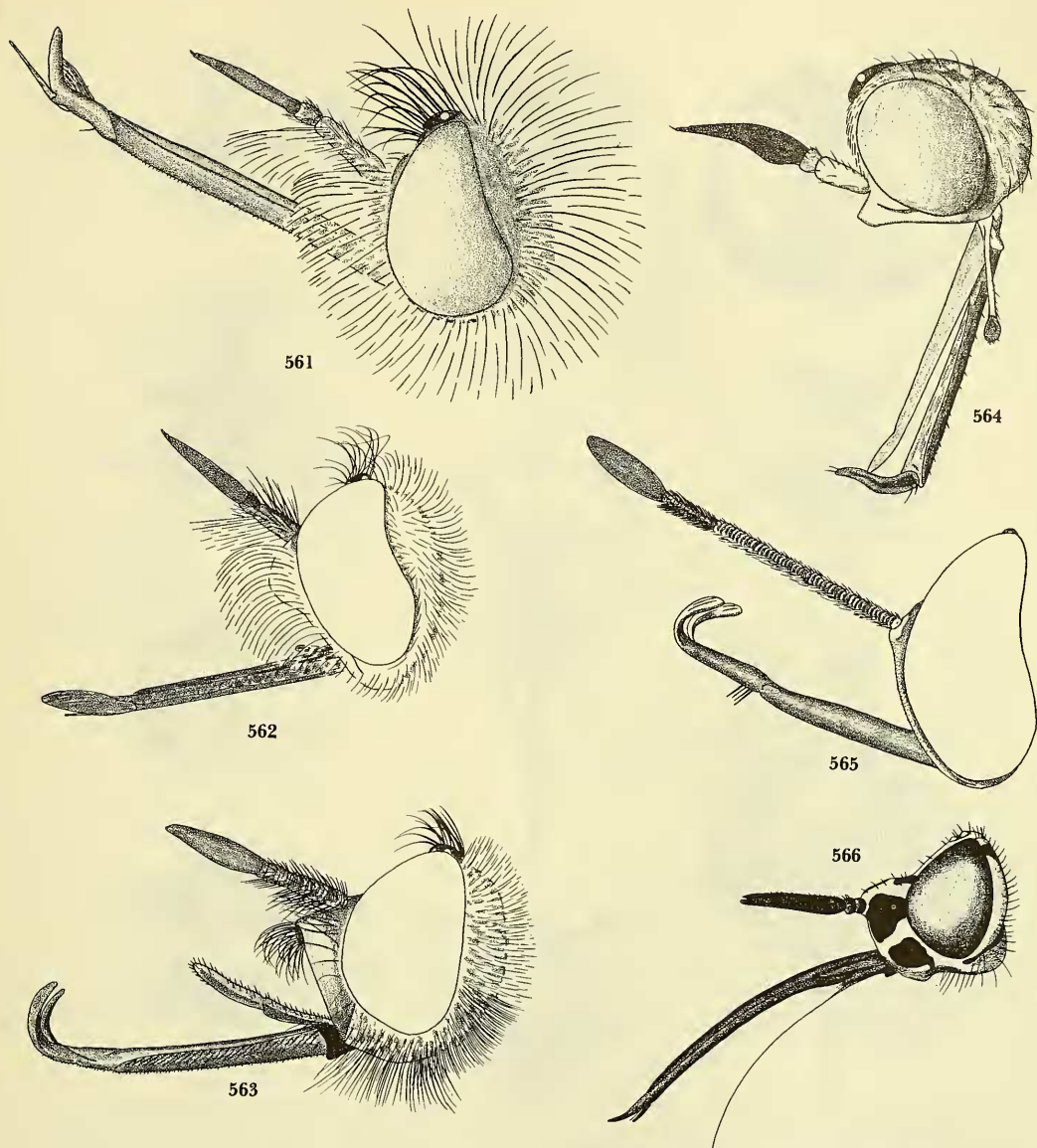
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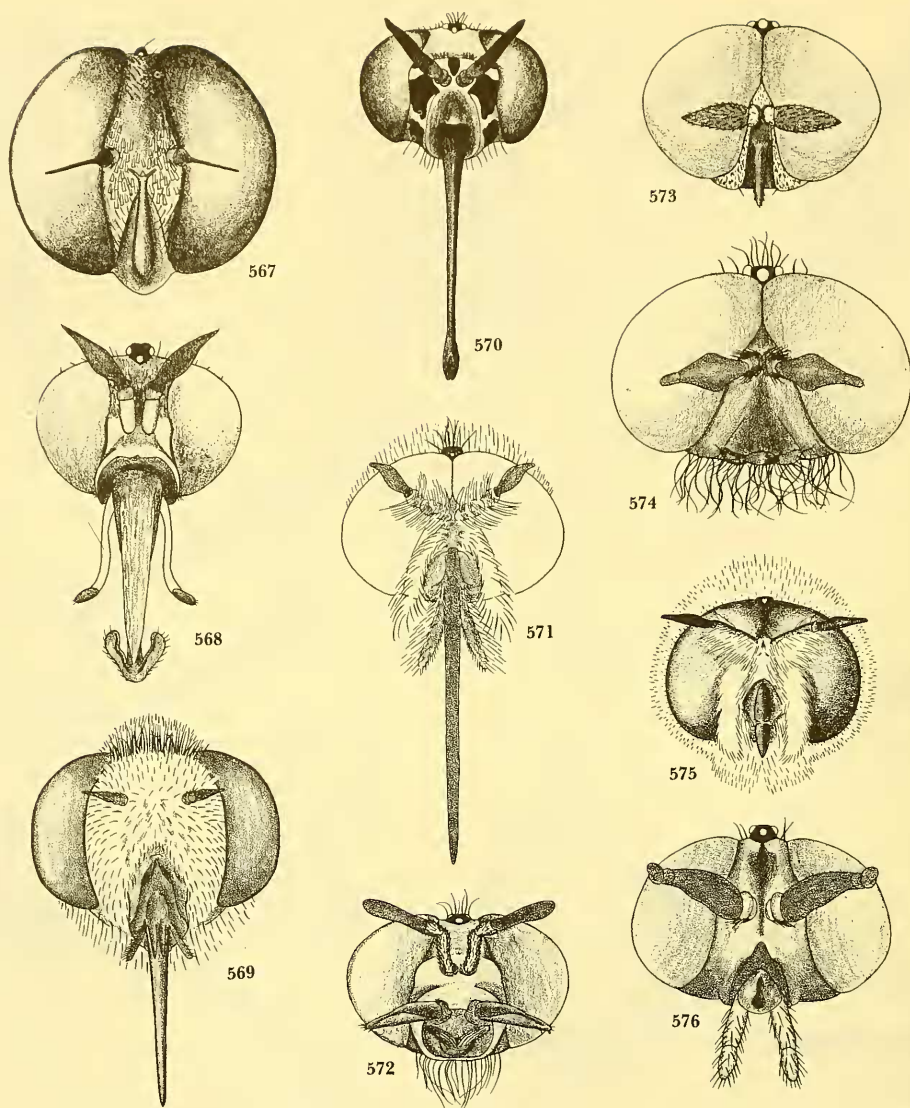
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554, *Oligodranes cincturus* Coquillett. 555, *Pseudo-*
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Rossi. 557, *Eflatounia* sp. 558, *Toxophora leuco-*

pyga Wiedemann. 559, *Heterostylum robustum*
Osten Sacken. 560, *Apolysis maherniaphila* Hesse,
type.



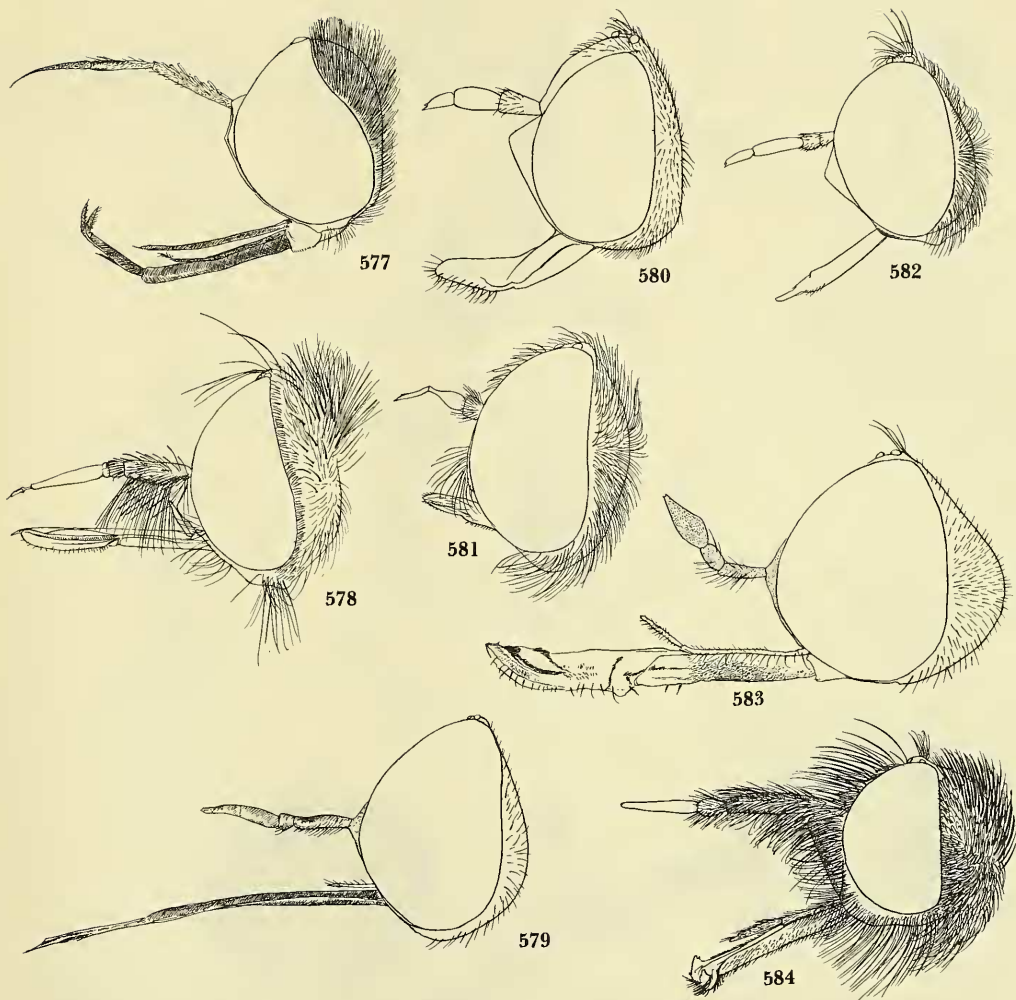
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Adelogenys culicoides Hesse. 565, *Systropus angulatus* Karsch. 566, *Phthiria* sp.



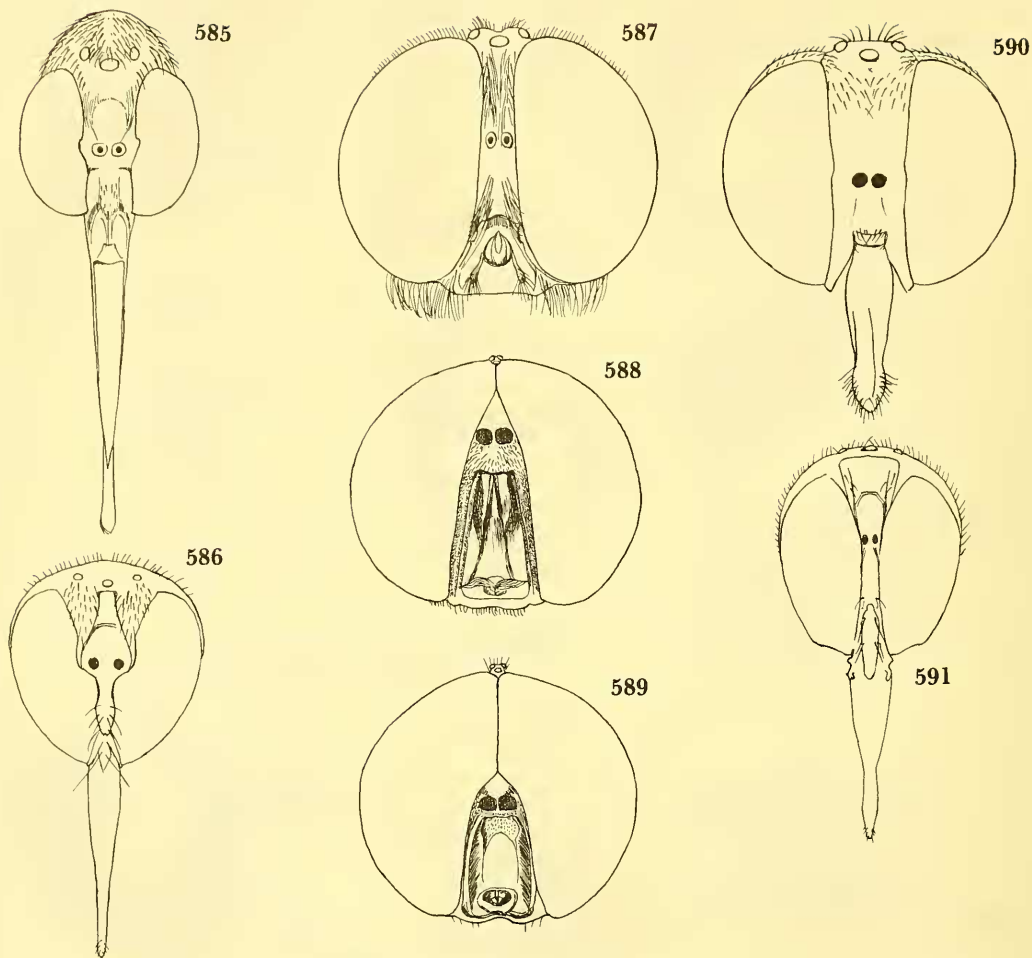
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573, *Prorates claripennis* Melander. 574, *Caenotus hospes* Melander. 575, *Lordotus gibbus* Loew. 576, *Desmatomyia anomala* Williston.



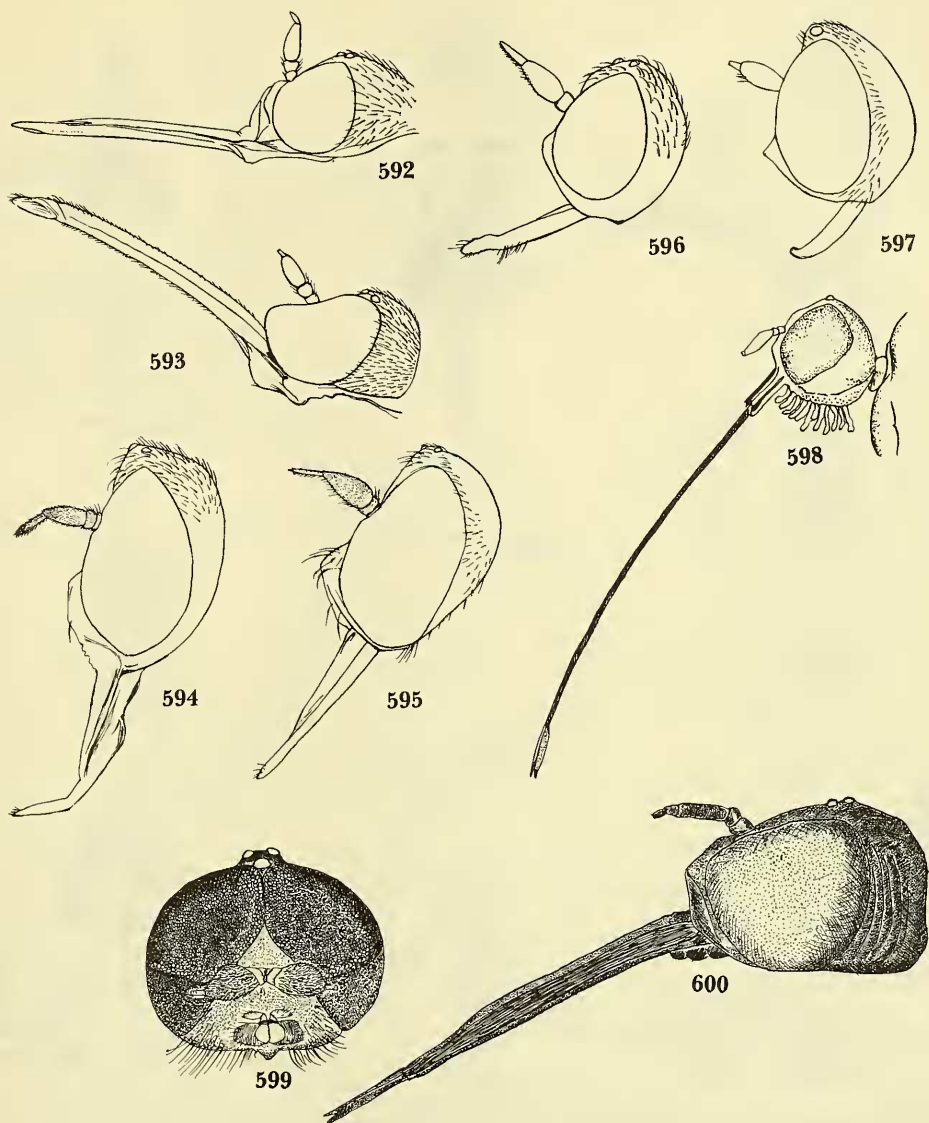
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White. 582, *Onchopelma pulchella* Hesse, type. 583, *Zaclava* sp. 584, *Cyrtomyia chilensis* Paramonov.



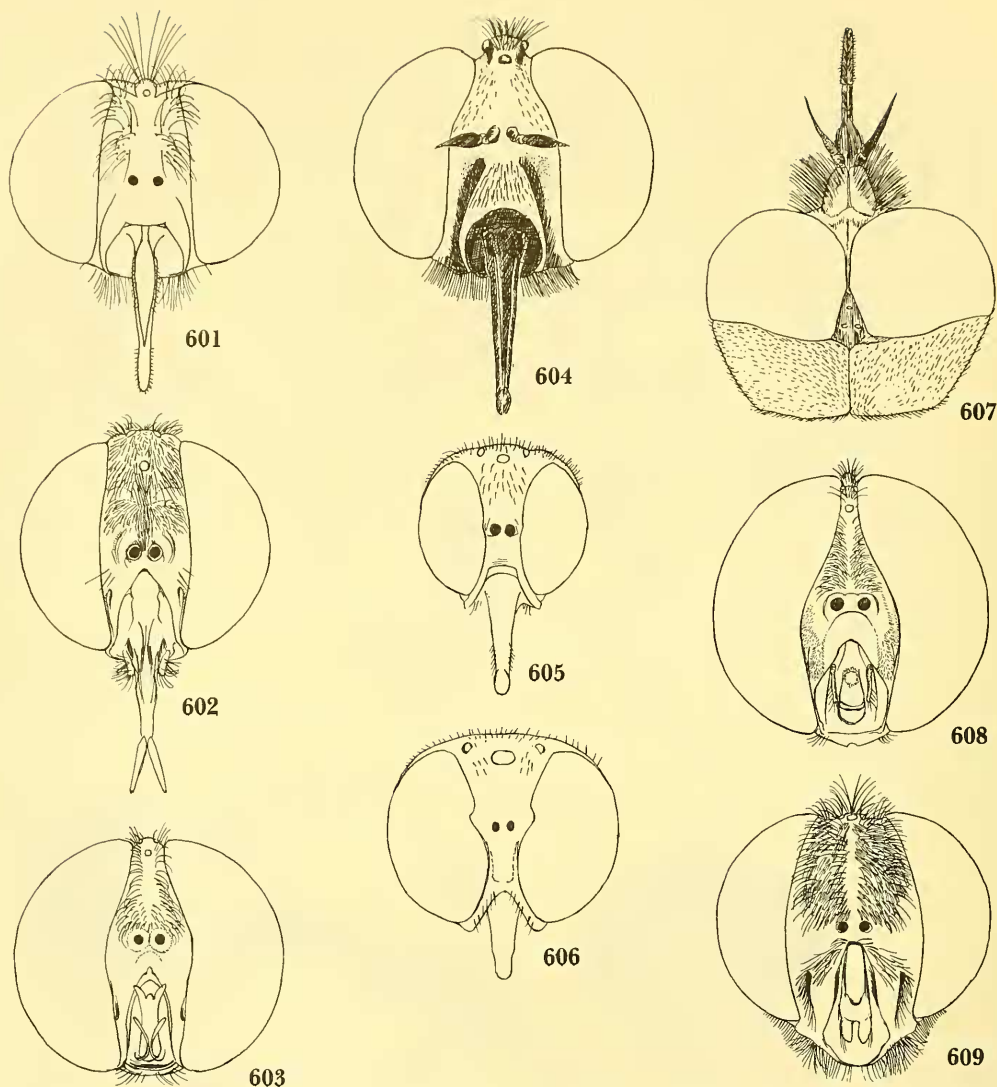
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589, *Dolichomyia gracilis* Williston. 590, *Onchopelma trilineata* Hesse, type. 591, *Empidideicus turneri* Hesse, allotype, female.



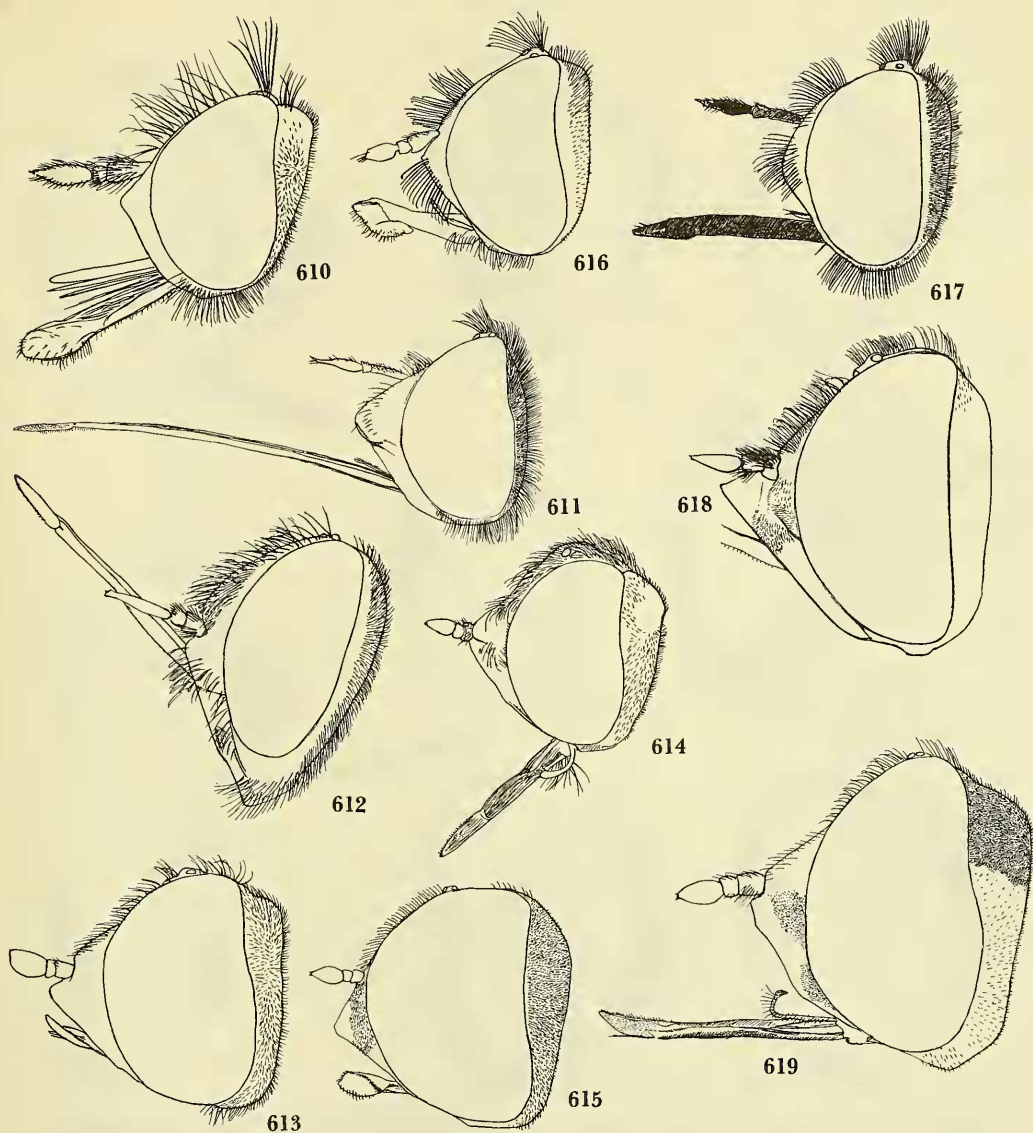
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Glabellula nobilis palaestinensis Engel. 598, *Euanthobates pectinigulus* Hesse. 599, *Apystomyia elinguis* Melander. 600, *Cyrtisiopsis crassirostris* Hesse.



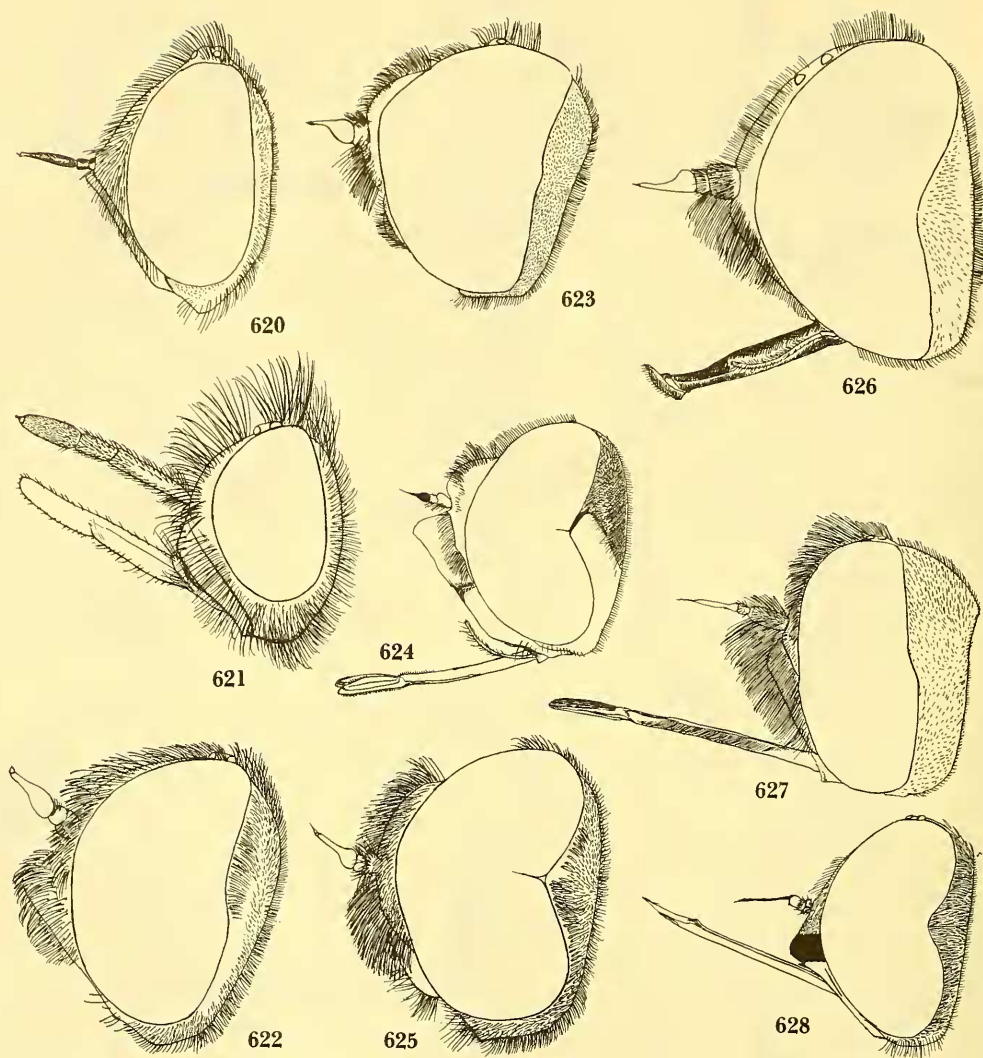
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606, *Glbellula nobilis palaestinensis* Engel. 607, *Peringueyimyia capensis* Bigot. 608, *Amphicosmus cincturus* Williston. 609, *Nomalonia afra* Macquart.



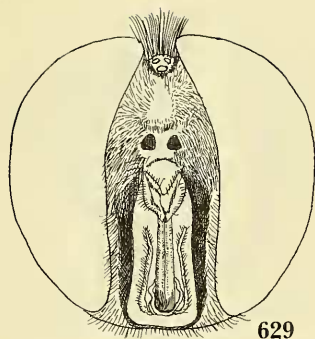
FIGURES 610-619.—610, *Sphenoidoptera varipennis* Williston, type. 611, *Amictus validus* Loew. 612, *Nomalonion afra* Macquart. 613, *Tomomyza pictipennis* Bezzi. 614, *Pantostomus tinctellipennis* Hesse, paratype. 615, *Metacosmus* sp. 616, *Cyl-*

lenia marginata Loew. 617, *Sinaia kneuckeri* Becker, after Eflatoun. 618, *Amphicosmus cincturus* Williston. 619, *Paracosmus morrisoni* Osten Sacken.

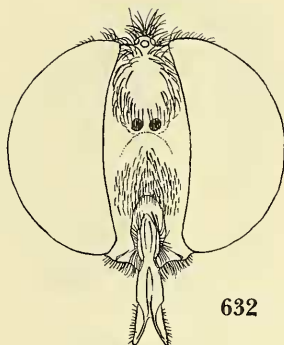


FIGURES 620-628.—620, *Henica longirostris* Wiedemann. 621, *Neosardus principius* Roberts. 622, *Prorostoma integrum* Bezzi. 623, *Docidomyia puellaris* White. 624, *Antonia suavissima* Loew.

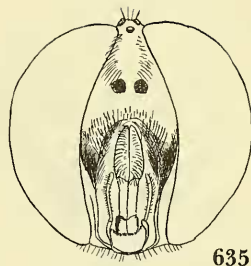
625, *Pteraulax flexicornis* Bezzi, male. 626, *Myonema* sp. 627, *Peringueyimyia capensis* Bigot. 628, *Epacmus litus* Coquillett.



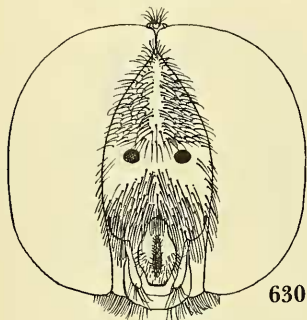
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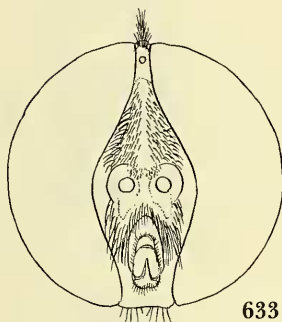
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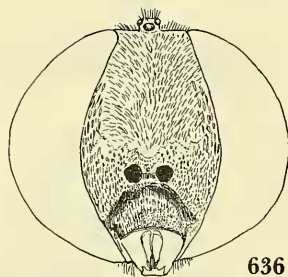
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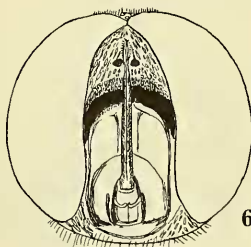
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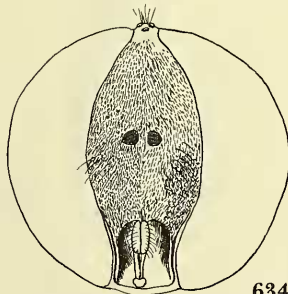
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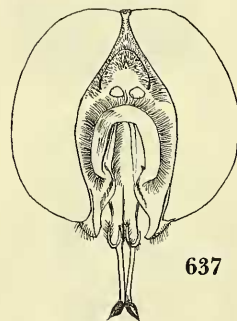
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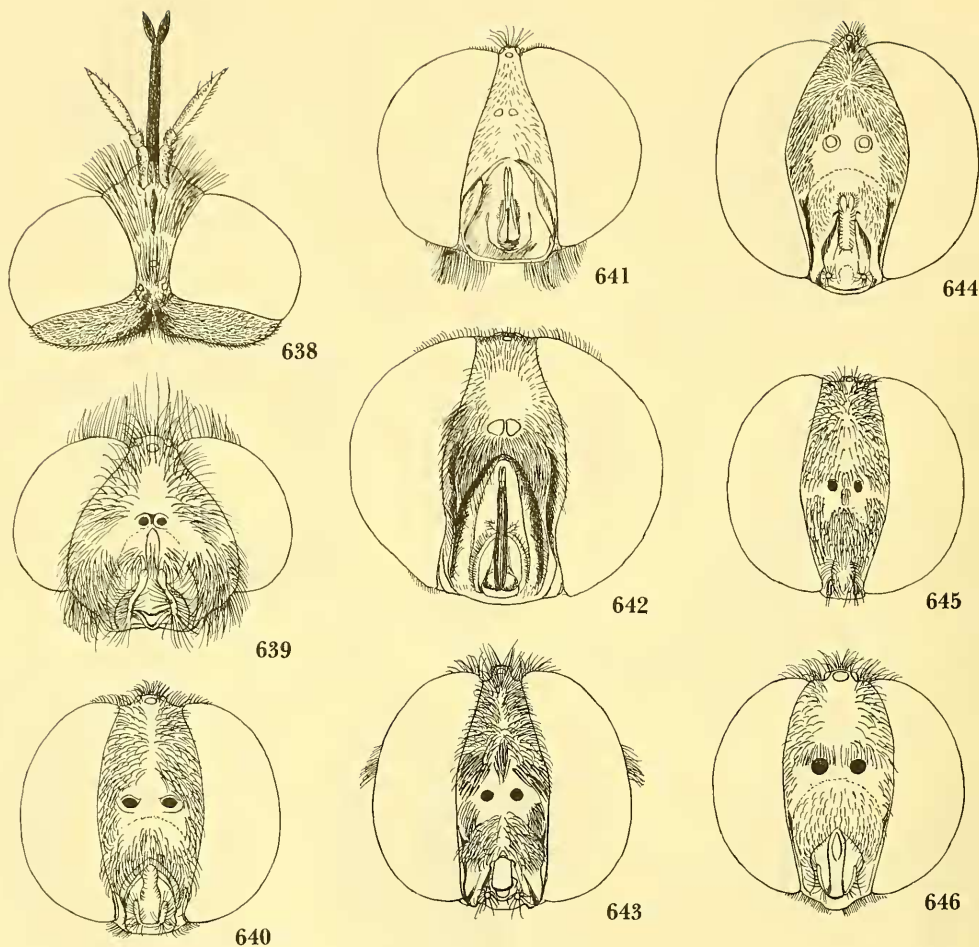
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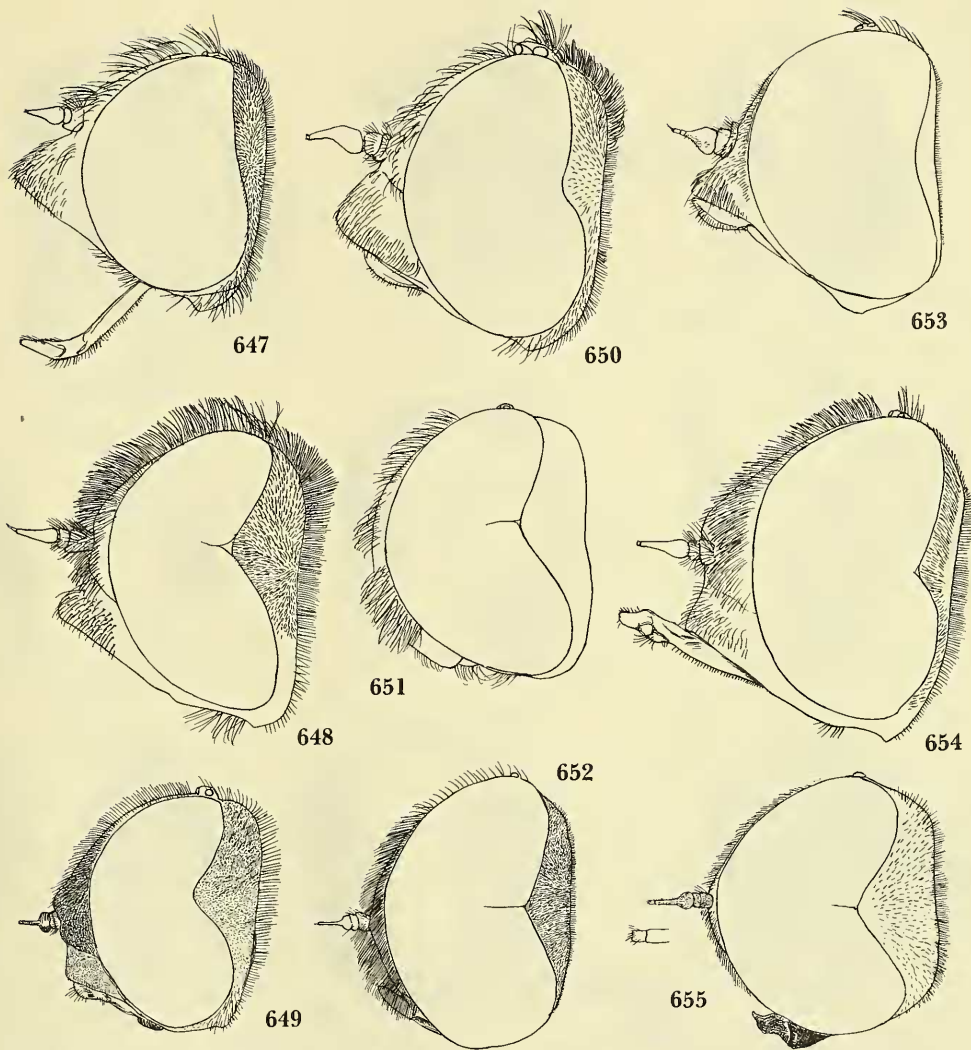
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Petrorossia letho Wiedemann. 635, *Eucessia rubens* Coquillett. 636, *Desmatoneura argentifrons* Williston. 637, *Antonia suavissima* Loew.



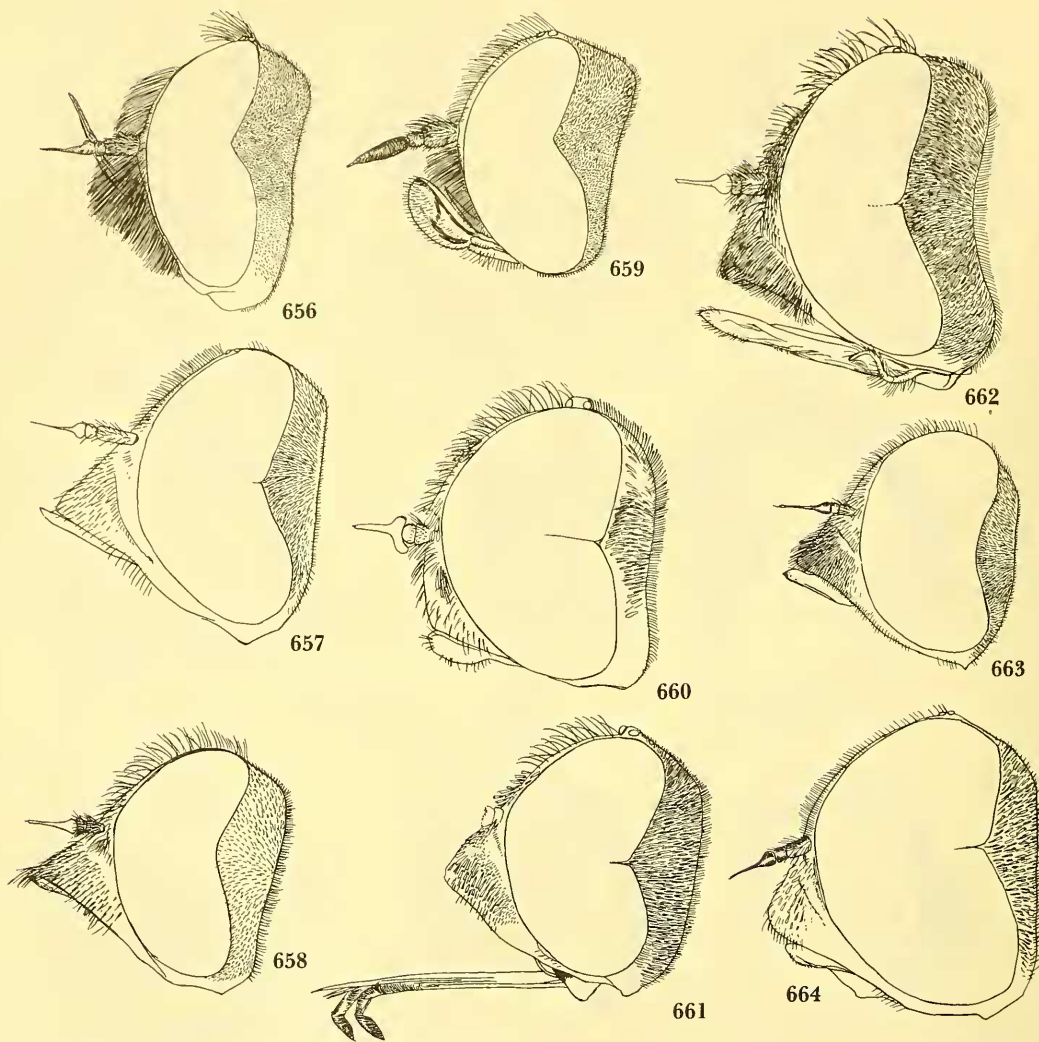
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sis Bigot. 643, *Plesiocera algira* Macquart. 644, *Chiasmella brevipennis* Bezzi. 645, *Chionamoeba sabulonis* Becker. 646, *Epacmoides albifrons* Hesse, paratype.



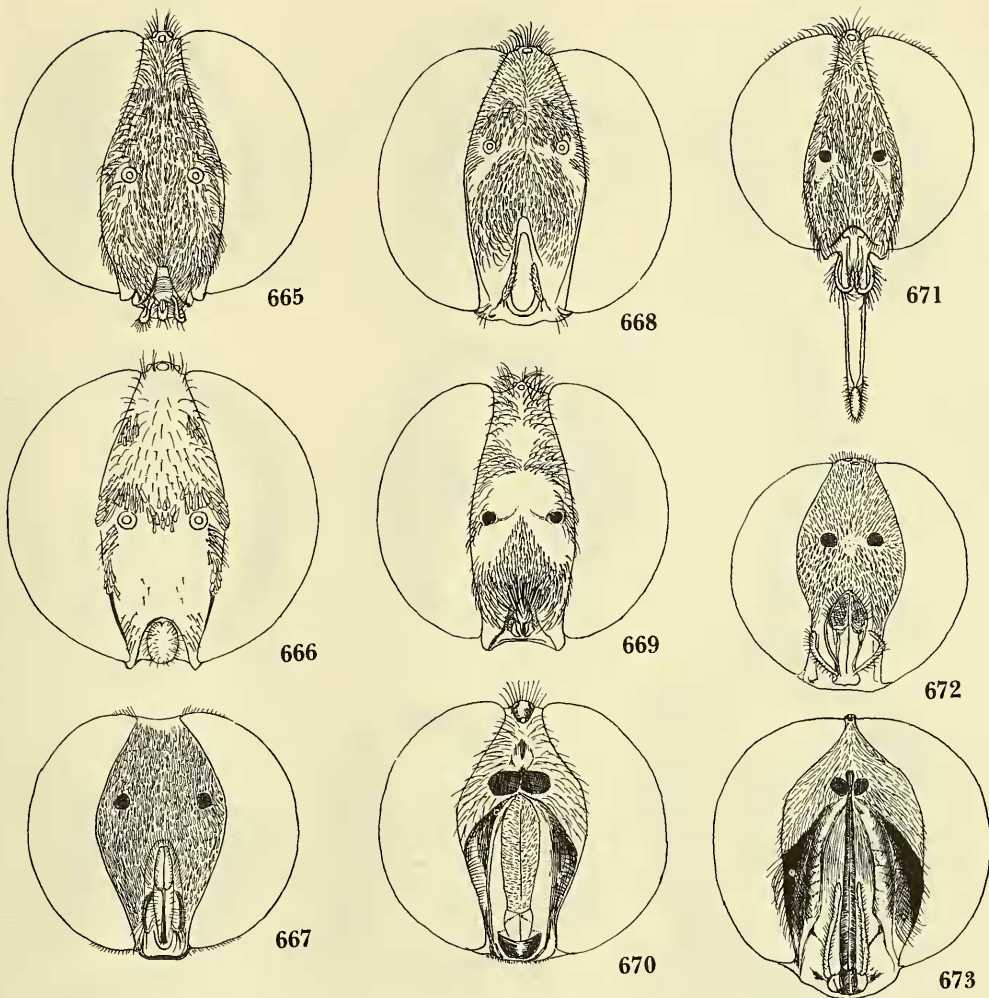
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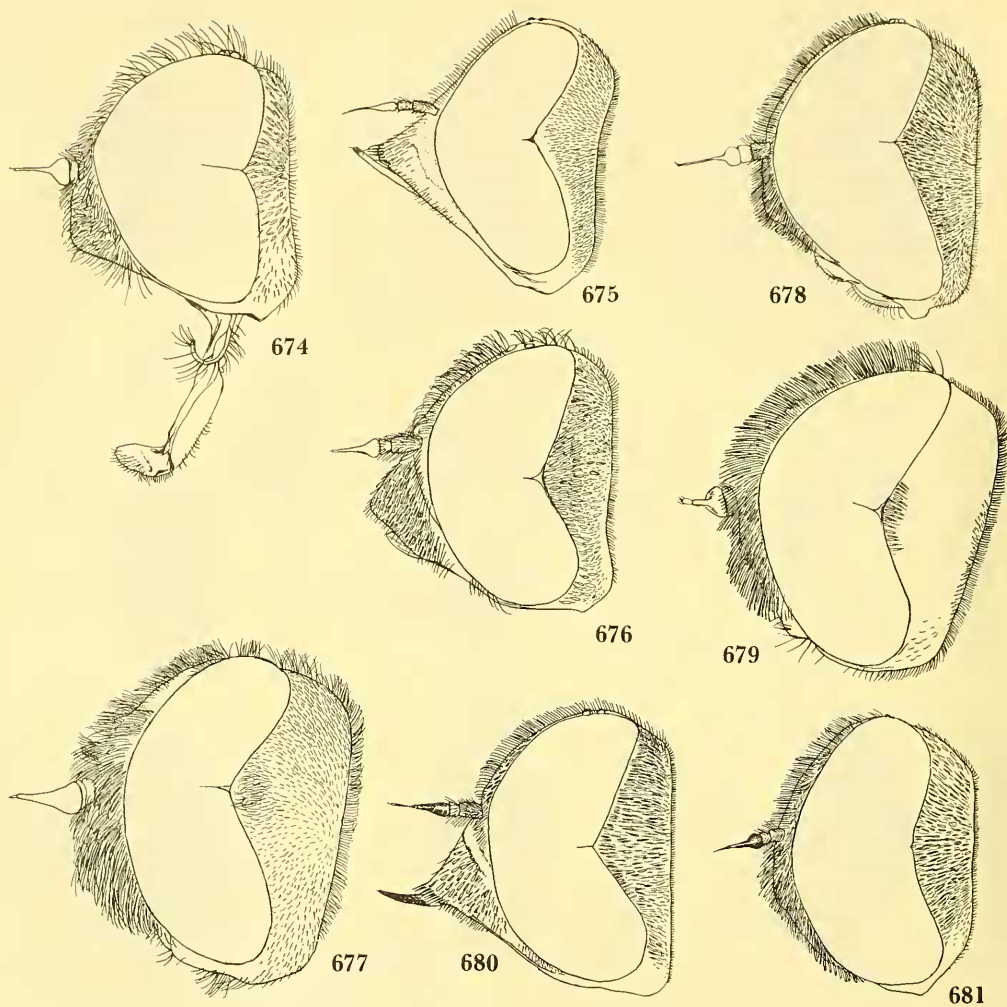
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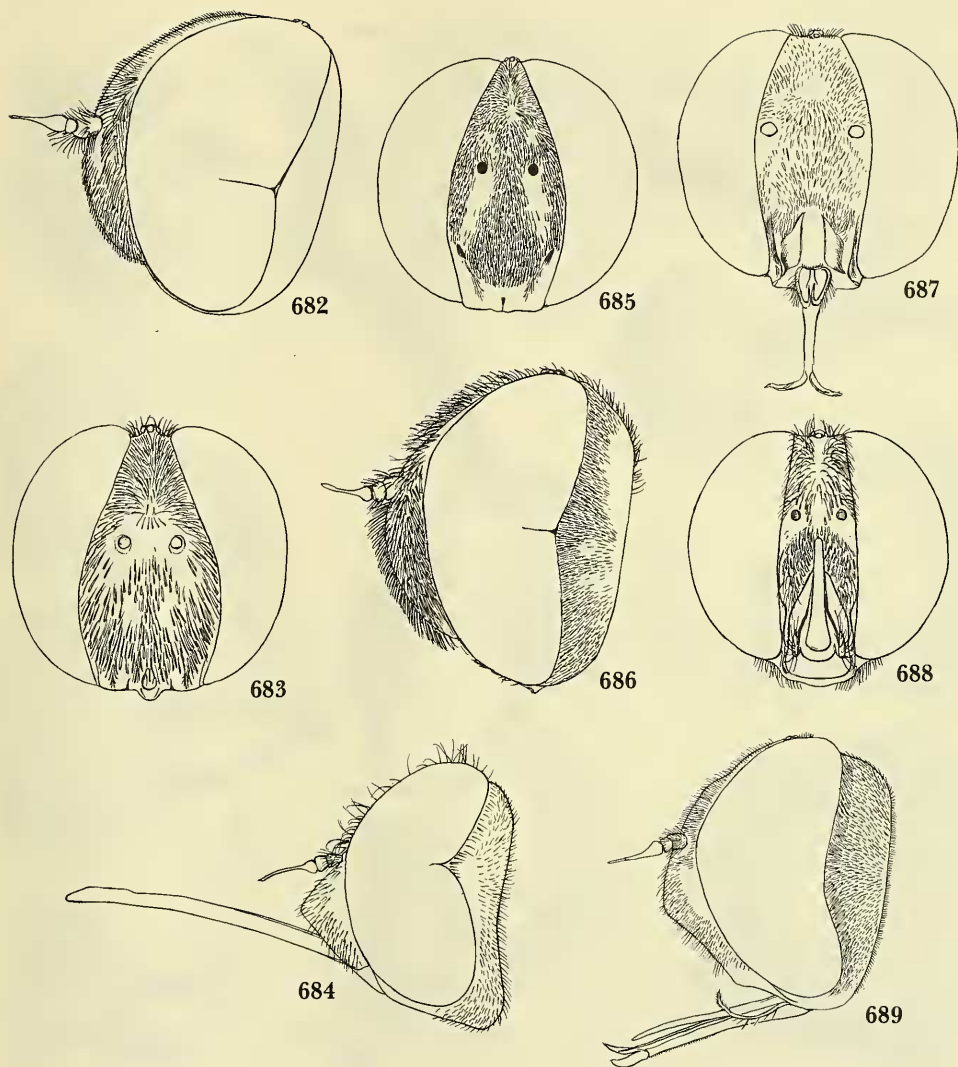
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Jaennicke. 670, *Ylasoia pegasus* Wiedemann. 671, *Diplocamptia secunda* Paramonov. 672, *Hemipenthes sinuosa* Wiedemann. 673, *Lyophlaeba (Macrocondyla) montana* Philippi.



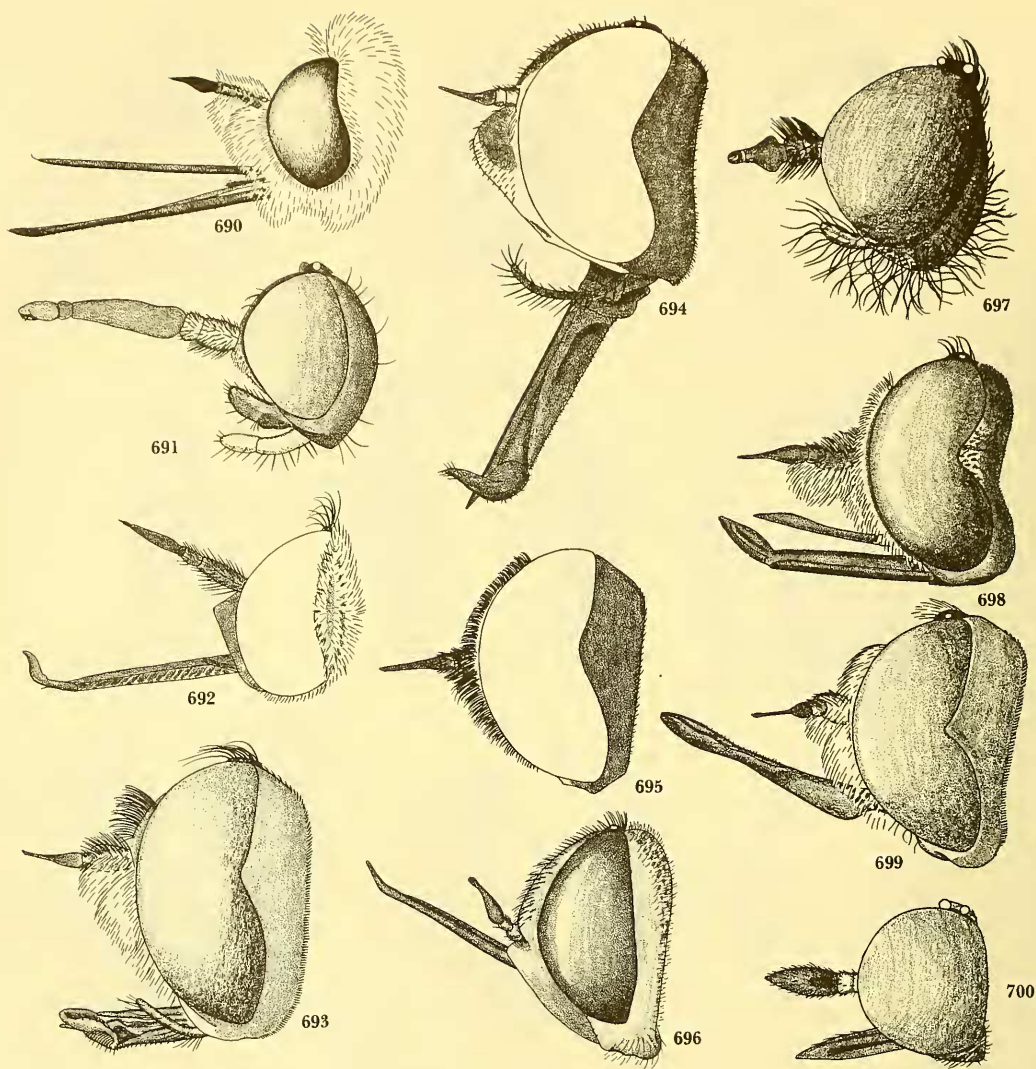
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sinuosa Wiedemann. 679, *Dicranoclista simpsoni* Bezzi, type. 680, *Exoprosopa jacchus* Fabricius. 681, *Villa pretiosa* Loew.



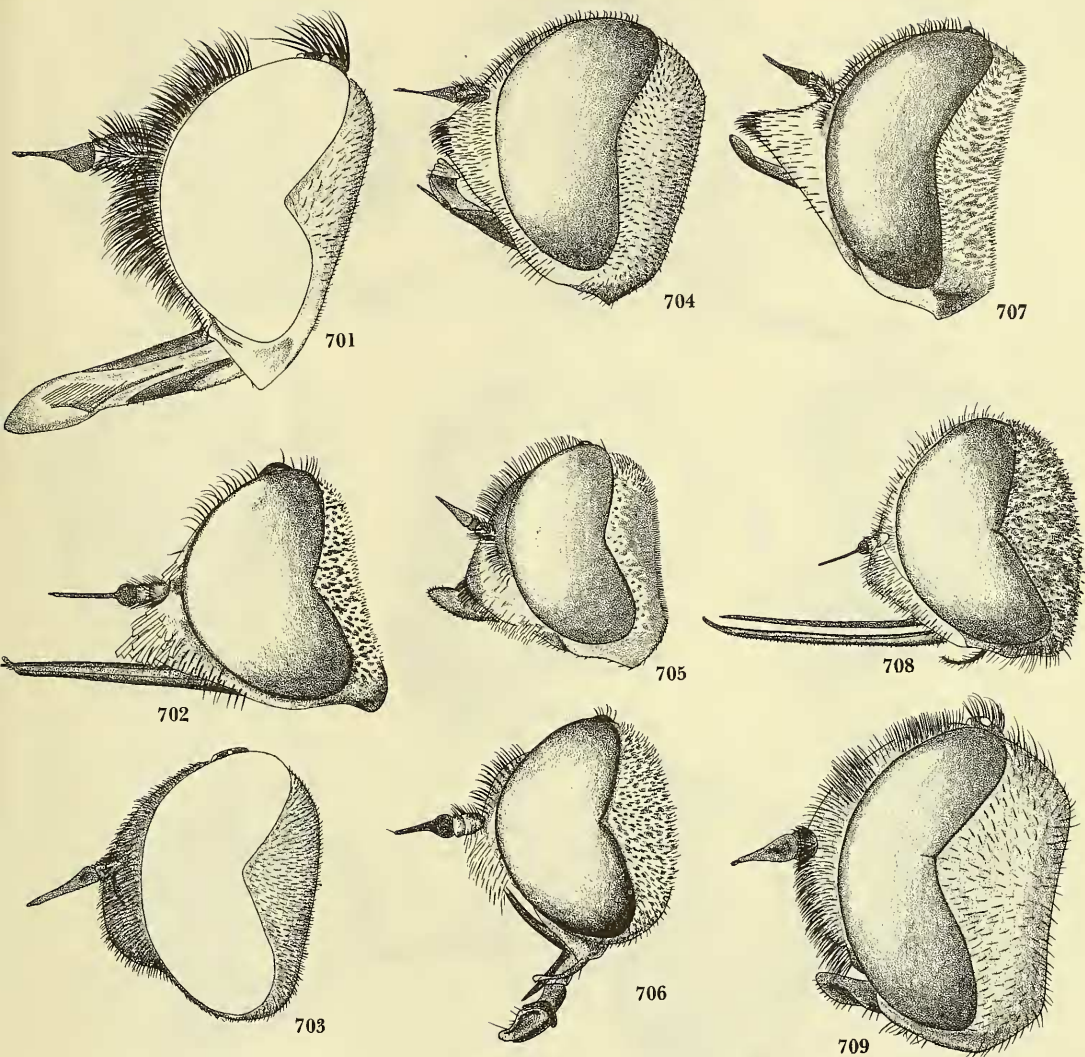
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obesus Loew. 687, *Litorrhynchus lar* Fabricius. 688, *Isotamia daveyi* Bezzi, type. 689, *Litorrhynchus lar* Fabricius.



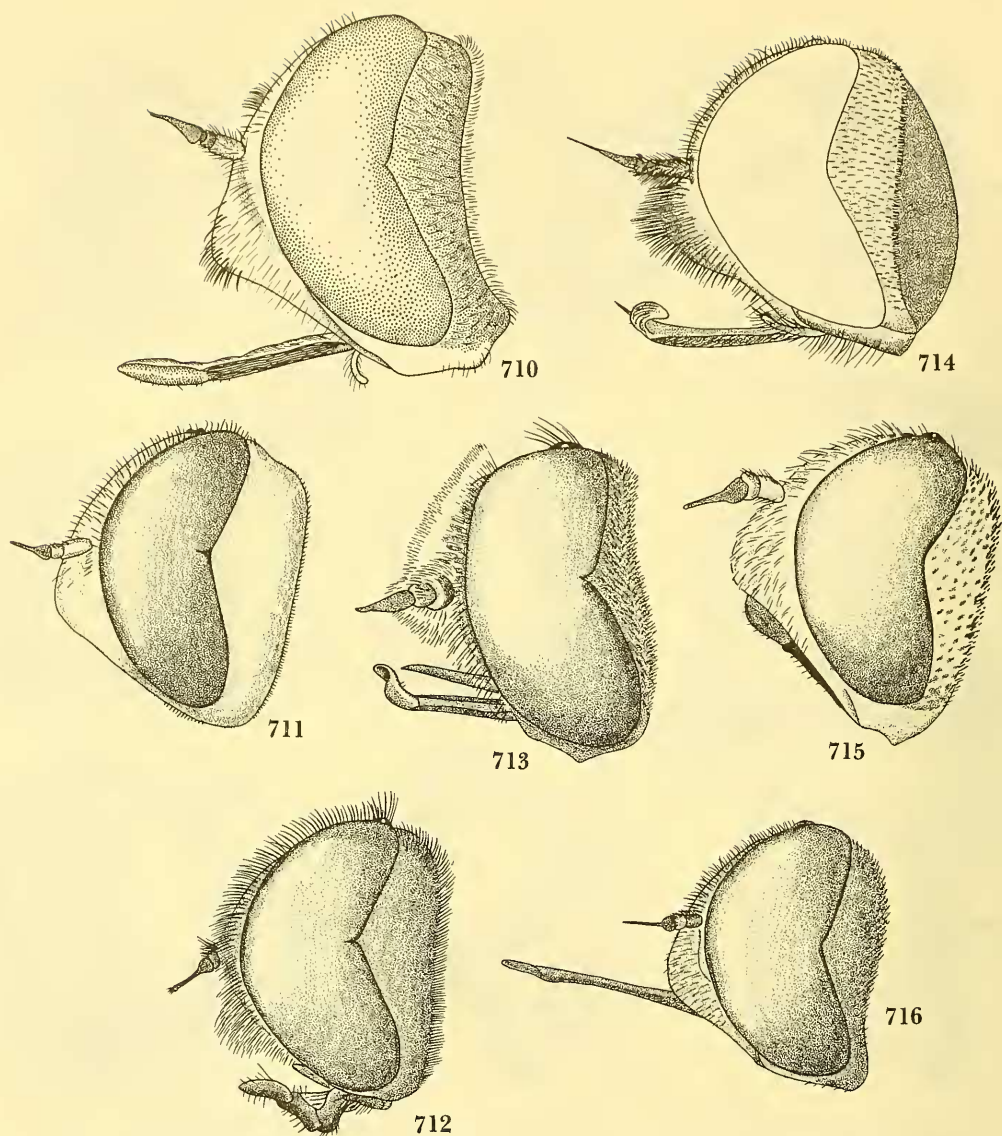
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valida Wiedemann. 696, *Nomalonia afra* Macquart. 697, *Caenotus hospes* Melander. 698, *Doddosia picta* Edwards. 699, *Oncodosia planus* Walker. 700, *Prorates claripennis* Melander.



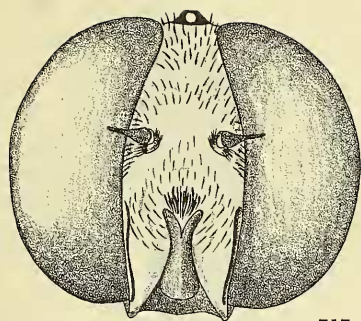
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702, *Lepidanthrax* sp. 703, *Oestrimyza fenestrata*,
new species. 704, *Ligyra tenebrosa* Paramonov.

705, *Thyridanthrax* sp. 706, *Aphoebantus* sp. 707,
Paravilla sp. 708, *Stonyx clotho* Wiedemann.
709, *Walkeromyia luridus* Walker.

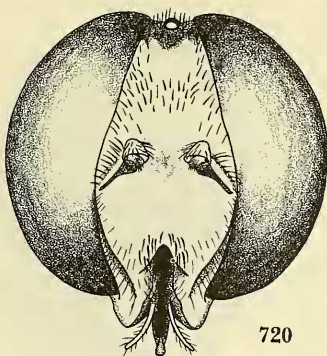


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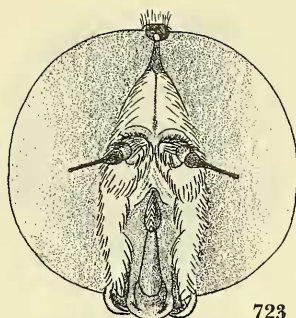
coprocta Wiedemann. 714, *Colossoptera latipennis* Brunetti. 715, *Synthesia fucoides* Bezzi. 716, *Rhynchanthrax parvicornis* Loew.



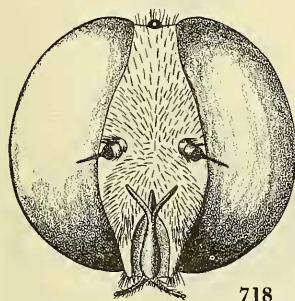
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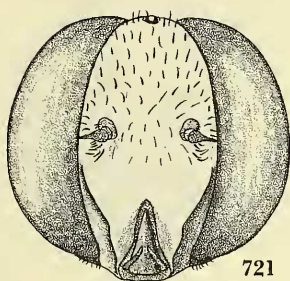
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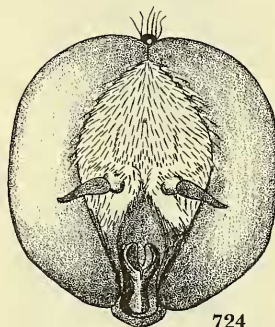
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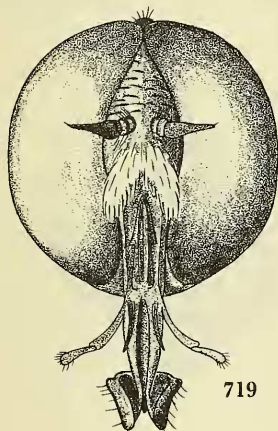
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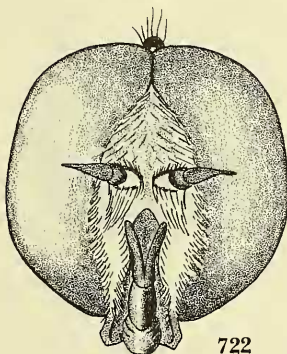
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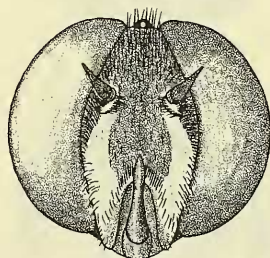
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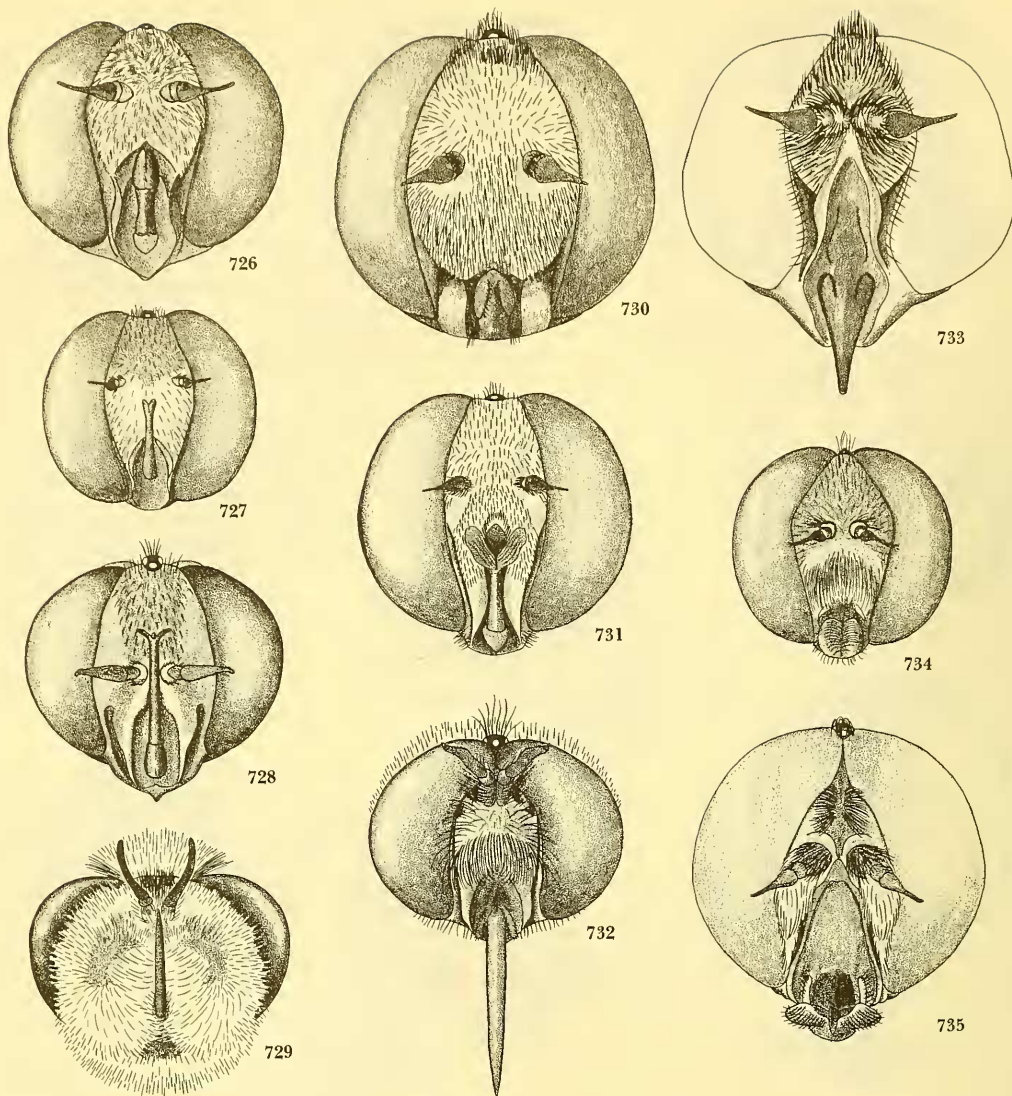
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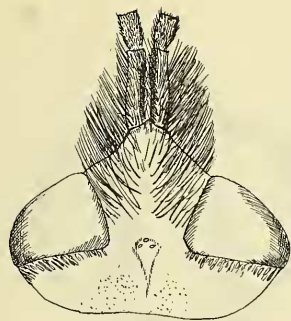
FIGURES 717-725.—717, *Parvilla* sp. 718, *Stonyx clotho* Wiedemann. 719, *Aphoebantus* sp. 720, *Poecilanthrax californicus* Cole. 721, *Atrichochira pediformis* Bezzi. 722, *Doddosia picta* Edwards.

723, *Oncodosia planus* Walker. 724, *Ogcodocera leucoprocta* Wiedemann. 725, *Thyridanthrax fenestratus* Fallén.

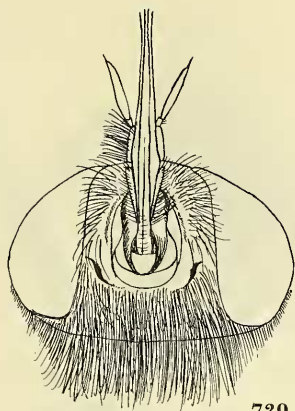


FIGURES 726-735.—726, *Synthesia fucoides* Bezzi. 727, *Rhynchanthrax parvicornis* Loew. 728, *Normalonia afra* Macquart. 729, *Corsomyza nigripes* Wiedemann. 730, *Walkeromyia luridus* Walker.

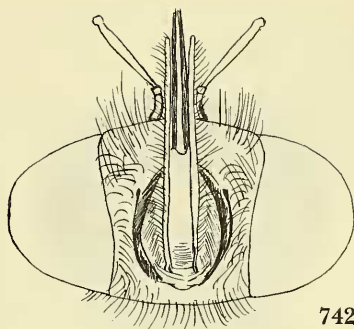
731, *Ligyra tenebrosa* Paramonov. 732, *Parabombylius coquilleti* Williston. 733, *Lomatia belzebul* Fabricius. 734, *Anthrax tigrinus* De Geer. 735, *Comptosia fascipennis* Macquart.



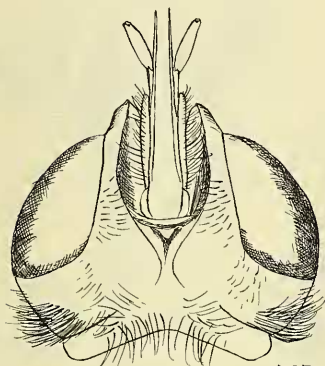
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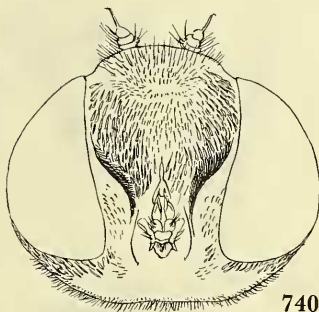
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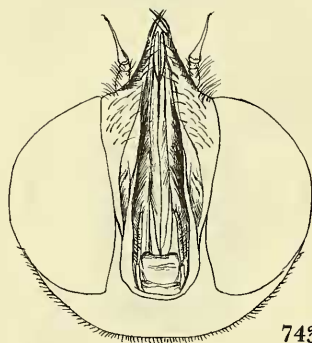
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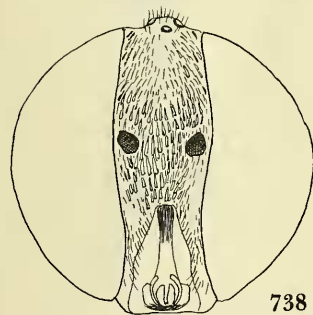
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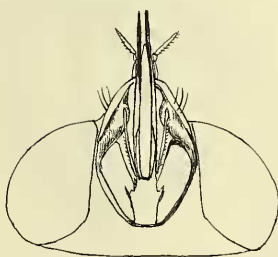
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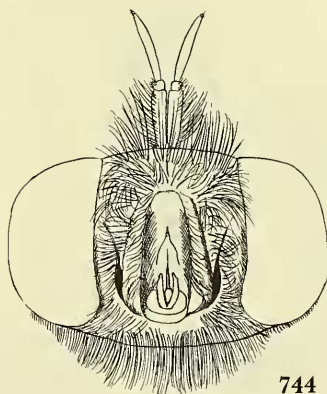
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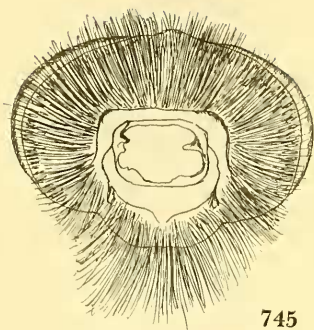
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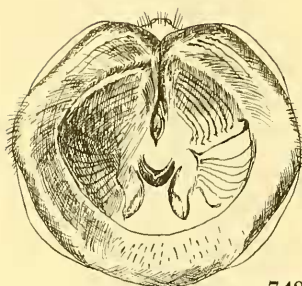
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FIGURES 736-744.—736, *Cyrtomyia chilensis* Paramonov, dorsal aspect. 737, *Oligodranes cincturus* Coquillett, ventral aspect. 738, *Mancina nana* Coquillett, frontal aspect. 739, *Adelidea anomala* Wiedemann, ventral aspect. 740, *Oestranthrax*

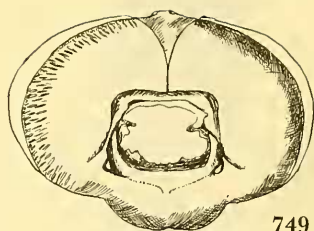
obesus Loew, ventral aspect. 741, *Amictus validus* Loew, ventral aspect. 742, *Megapalpus capensis* Wiedemann, ventral aspect. 743, *Neodiplocamptia paradoxa* Jaennicke, ventral aspect. 744, *Doliogethes* sp., ventral aspect.



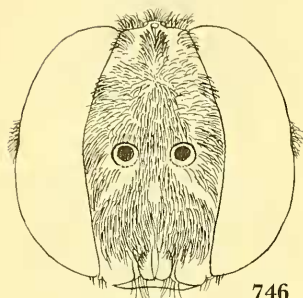
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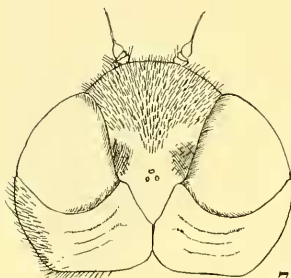
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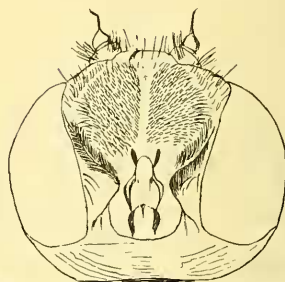
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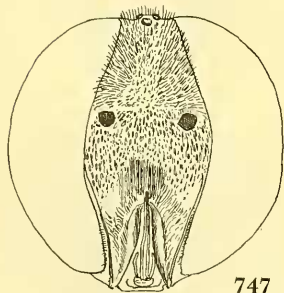
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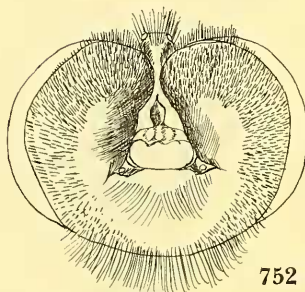
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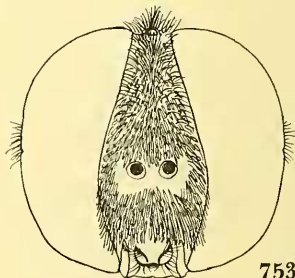
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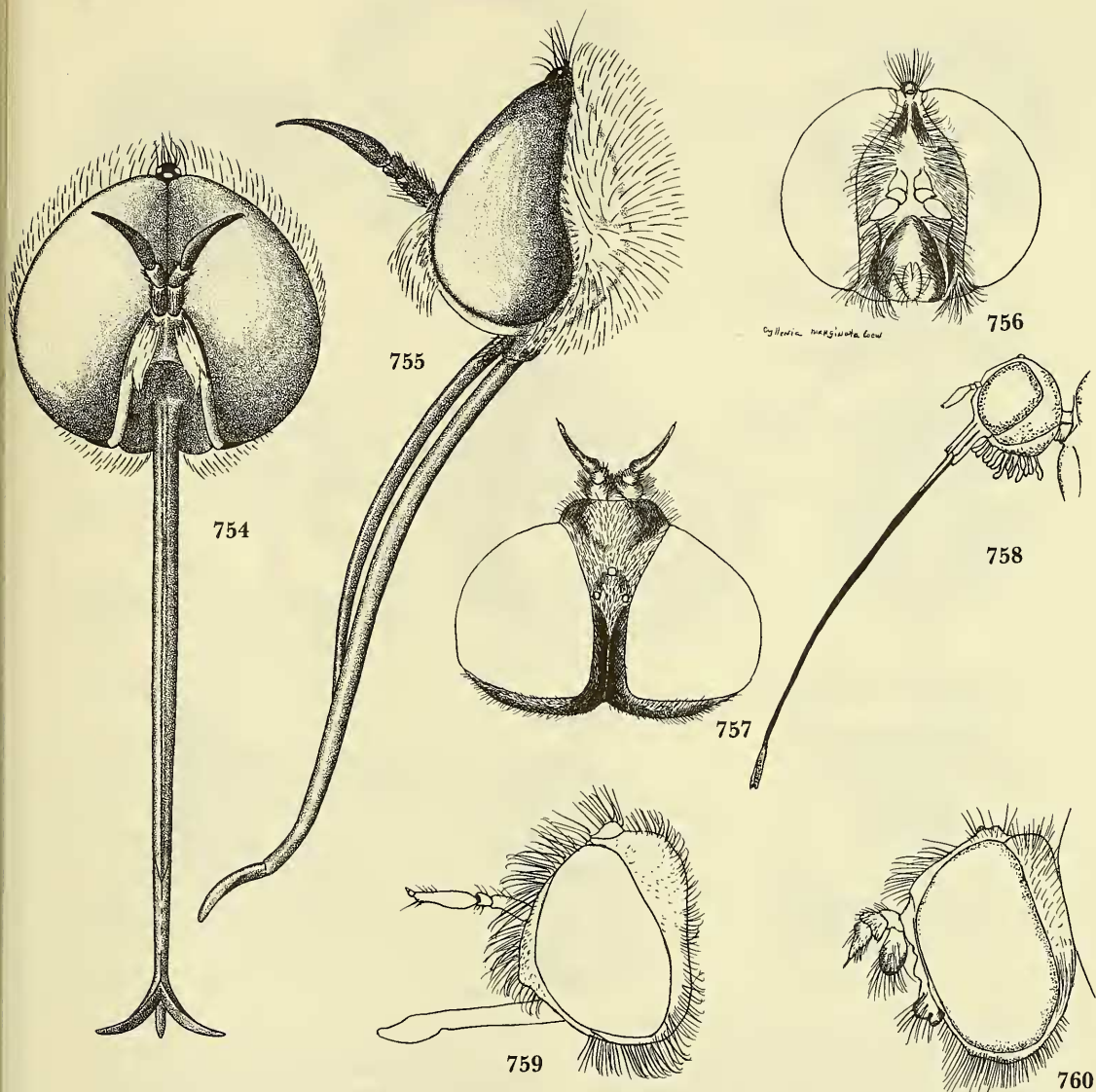
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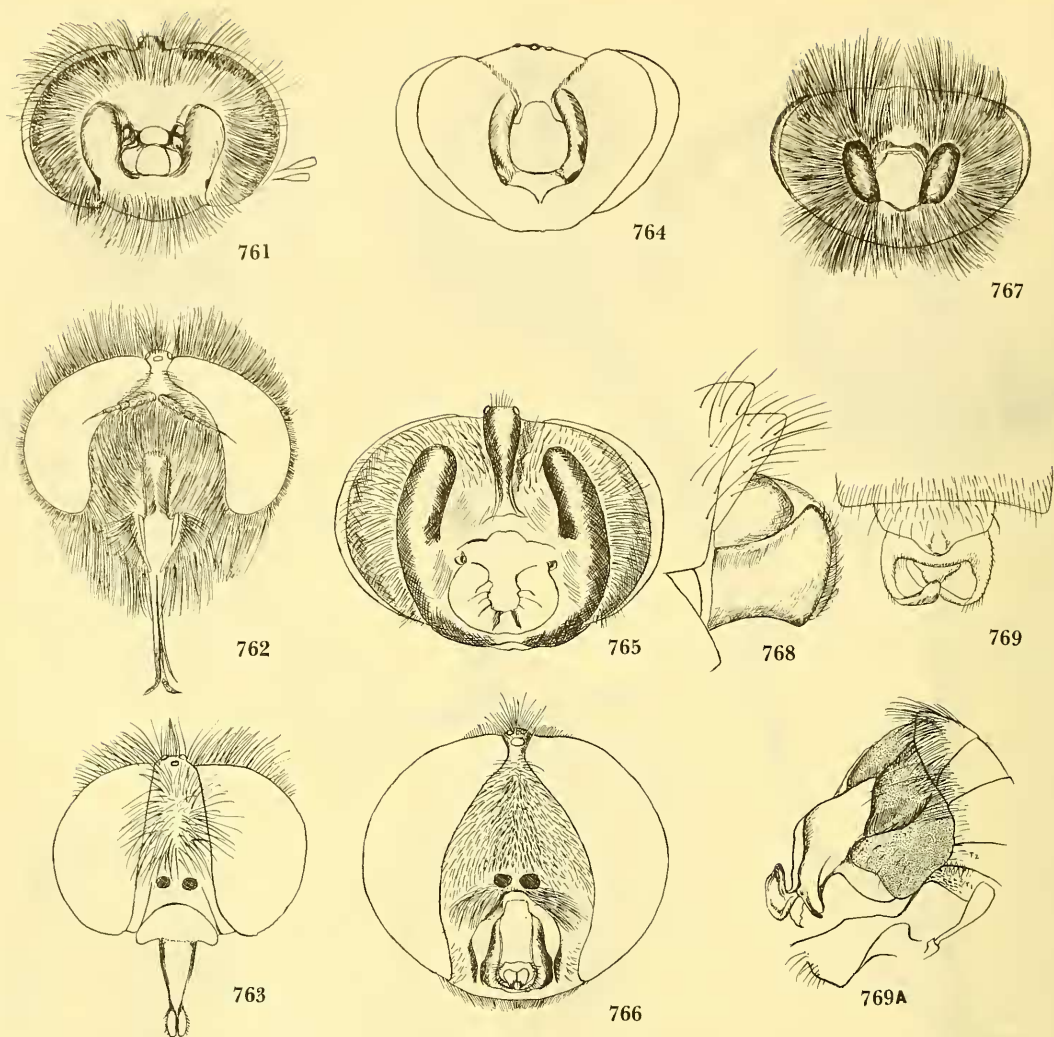
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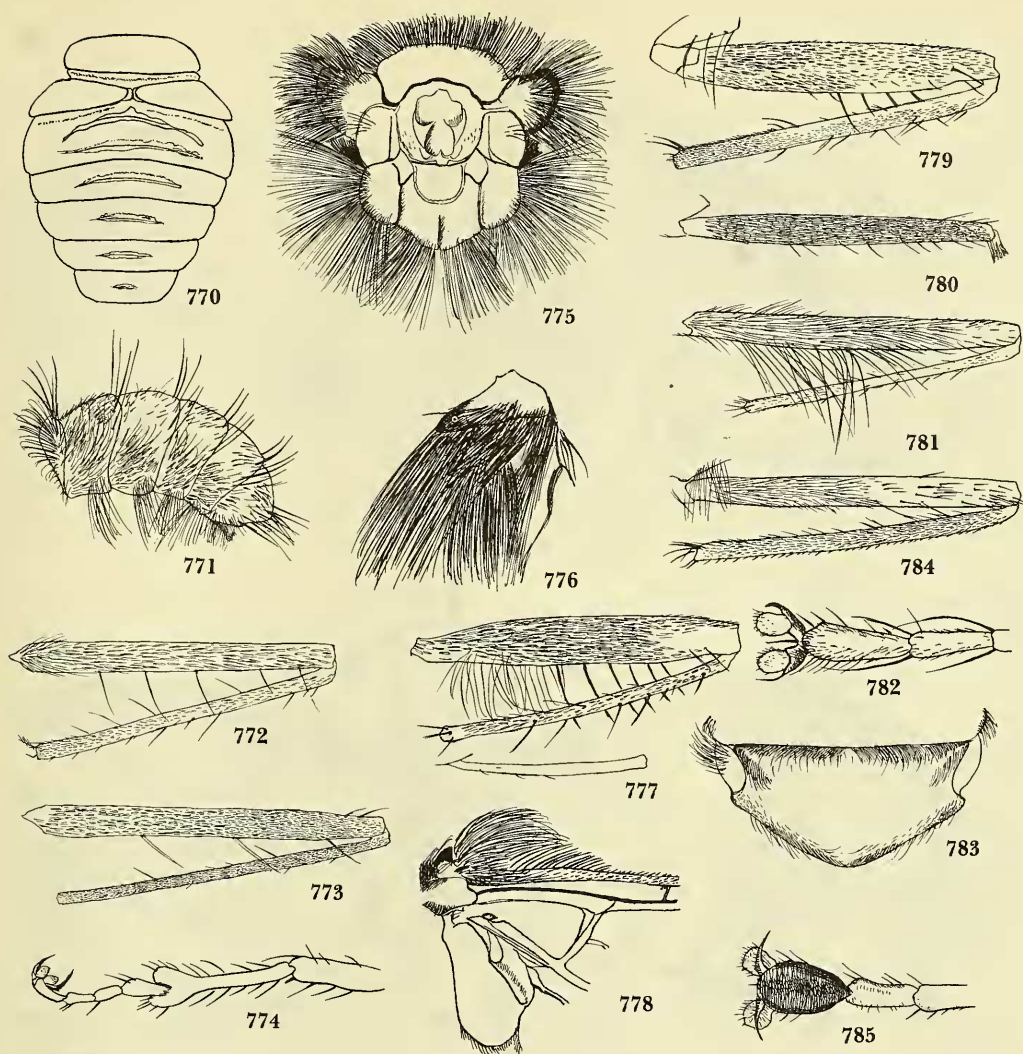
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755, *Geron* sp. New Mexico. 756, *Cyllenina margi-*
nata Loew. 757, *Myonema humilis* Roberts.

Euanthobates pectinigulus Hesse, after Hesse.
759, *Sinaia kneuckeri* Becker, after Engel. 760,
Xenoprosopa paradoxa Hesse, after Hesse.



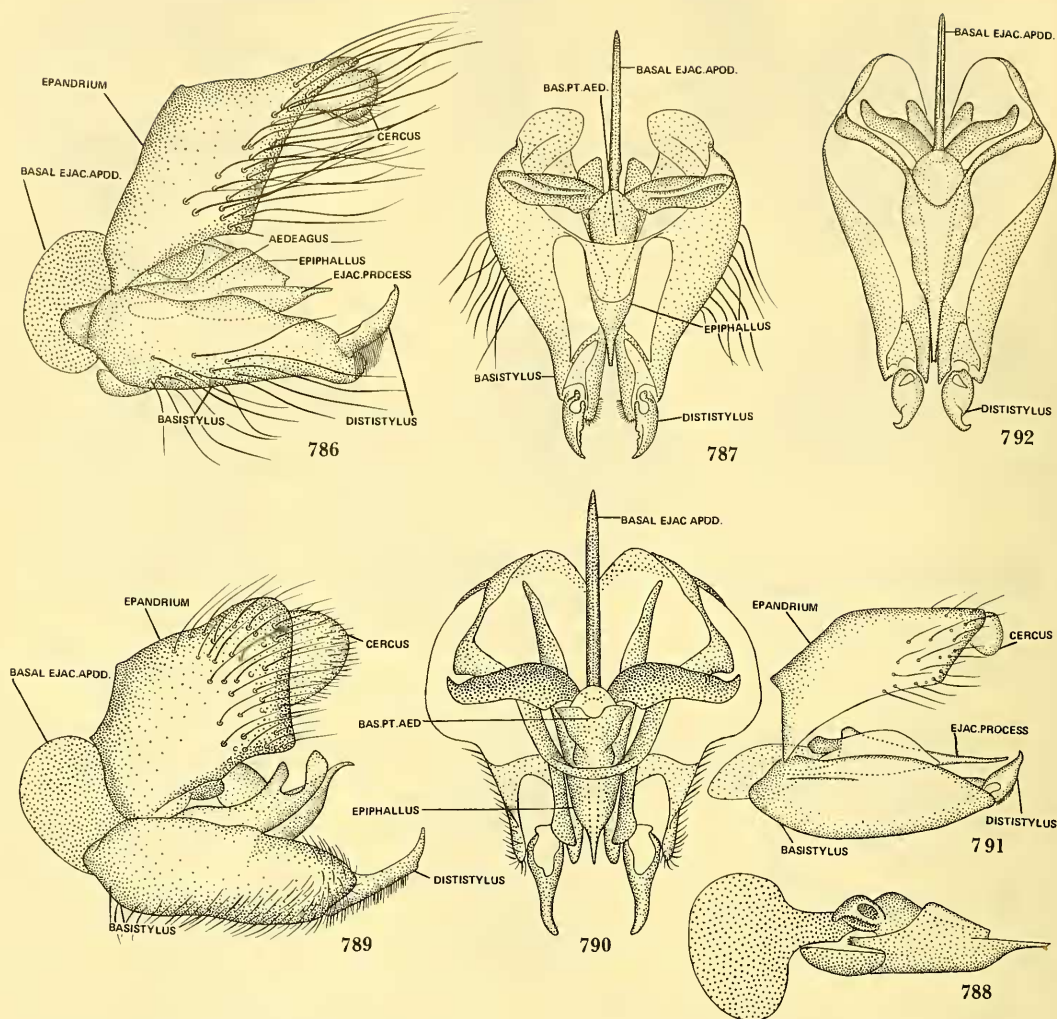
FIGURES 761-769A.—761, *Lepidochlanus fimbriatus* Hesse. 762, *Acanthogeron senex* Meigen. 763, *Tillardomyia gracilis* Tonnoir. 764, *Megapalpus capensis* Wiedemann. 765, *Oligodranes cincturus* Coquillett. 766, *Henica longirostris* Wiedemann.

767, *Sericusia lanata* Edwards, from type. 768, *Acrophthalmyda sphenoptera* Loew, male genitalia. 769, *Antonia rieki* Paramonov, female genitalia. 769A, *Usia florea* Fabricius, male genitalia.



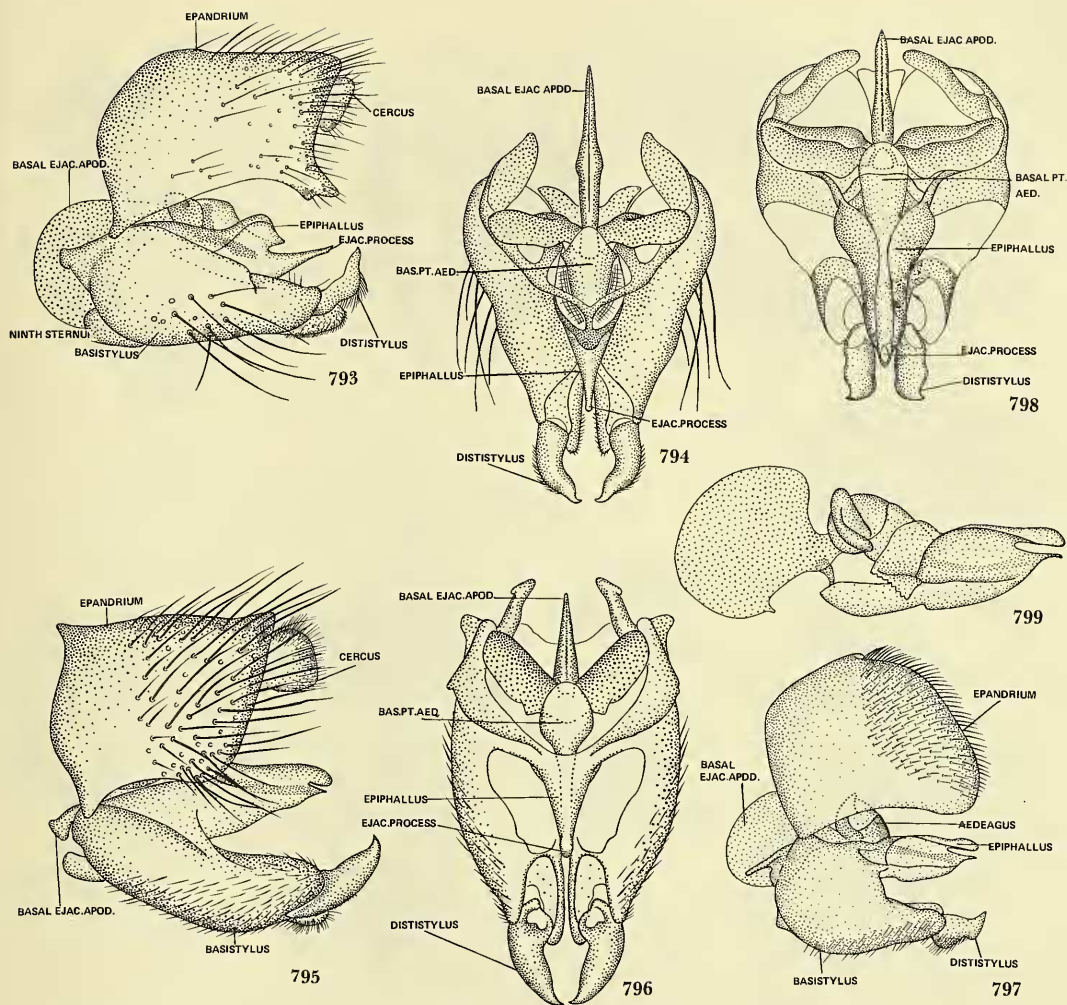
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costal hook and comb. 779, *Amictus validus* Loew, hind femur. 780, *Anastoechus trisignatus* Portschinsky, hind femur. 781, *Lissomerus niveicomatus* Austen, type, hind femur. 782, *Heterotropus arenivagus* Paramonov, hind tarsus, after Engel. 783, *Oestranthrax obesus* Loew, scutellum. 784, *Acanthogeron senex* Wiedemann, hind femur. 785, *Heterotropus arenivagus* Paramonov, anterior tarsus, after Engel.



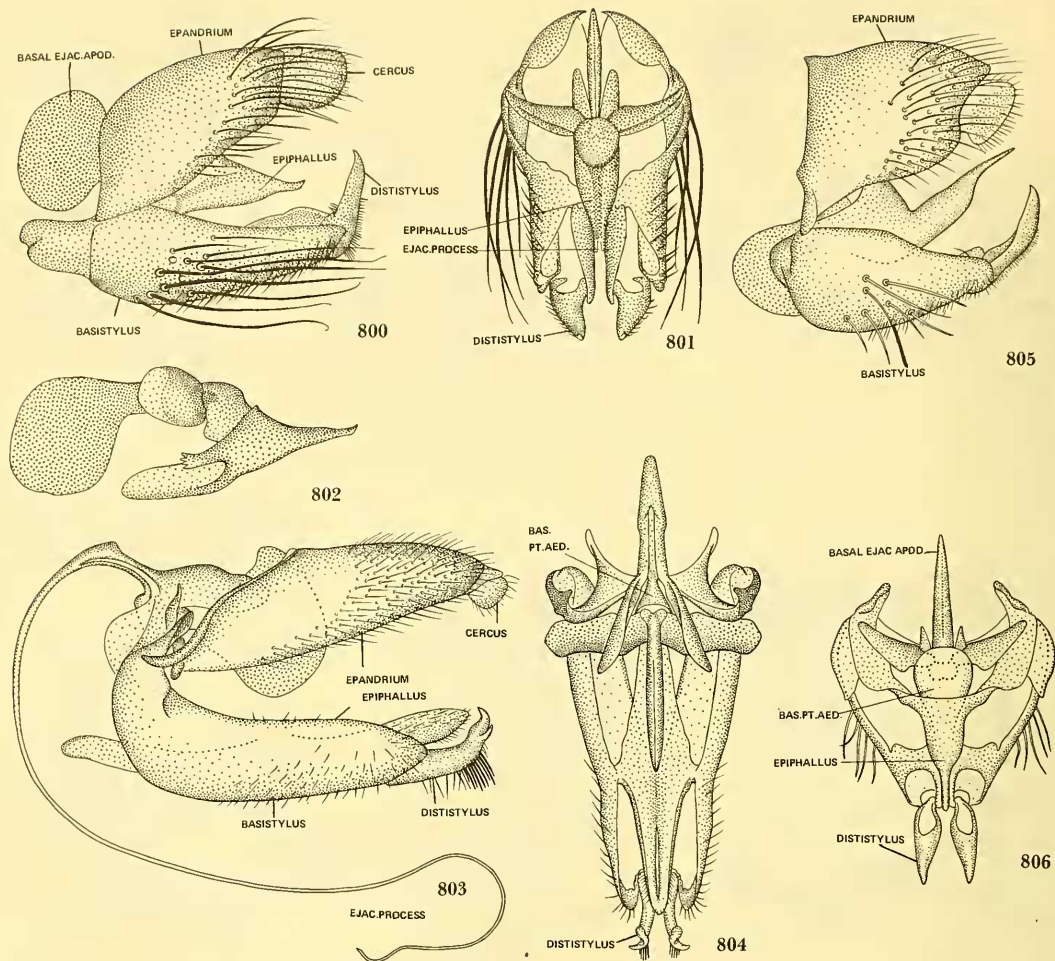
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aspect. 790, *Systoechus vulgaris* Osten Sacken, dorsal aspect. 791, *Anastoechus barbatus* Osten Sacken, lateral aspect. 792, *Anastoechus barbatus* Osten Sacken, dorsal aspect.



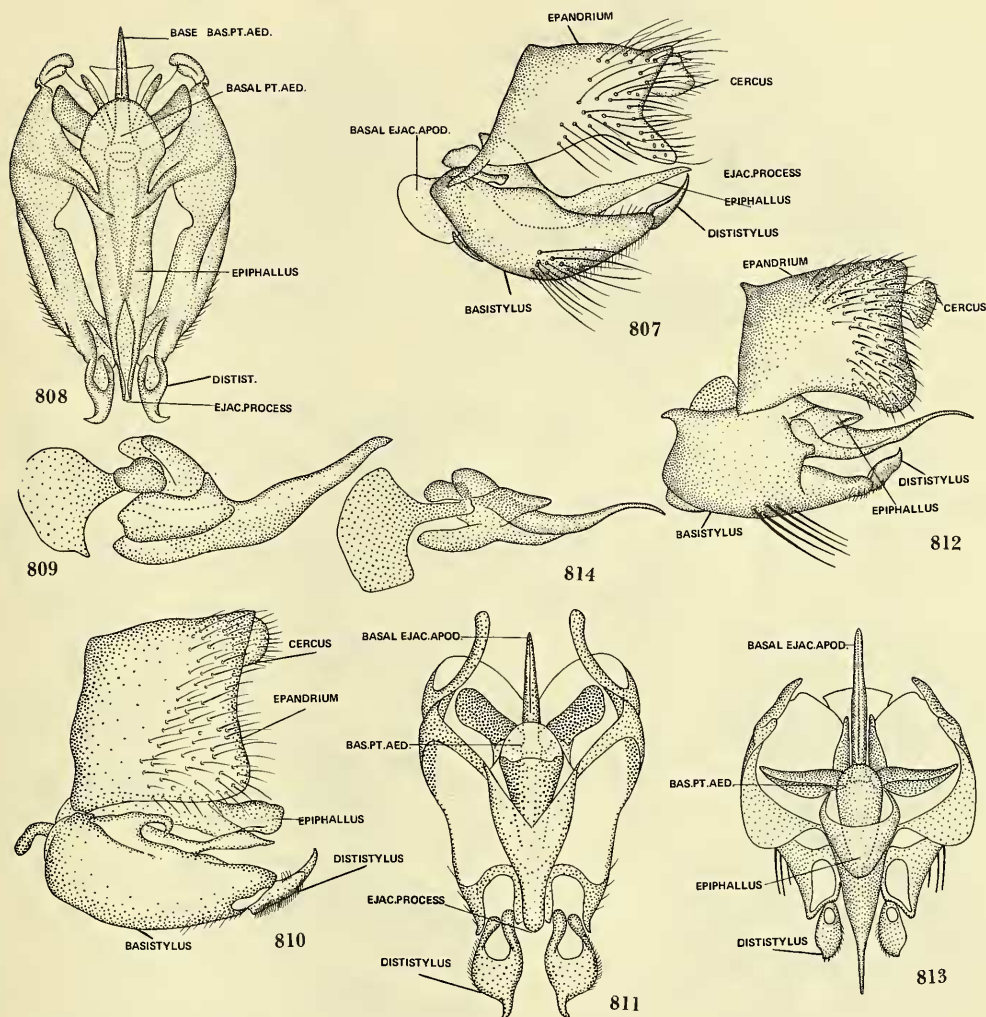
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celer Cole, dorsal aspect. 797, *Acrophthalmyda sphenoptera* Loew, lateral aspect. 798, *Acrophthalmyda sphenoptera* Loew, dorsal aspect. 799, *Acrophthalmyda sphenoptera* Loew, axial system.



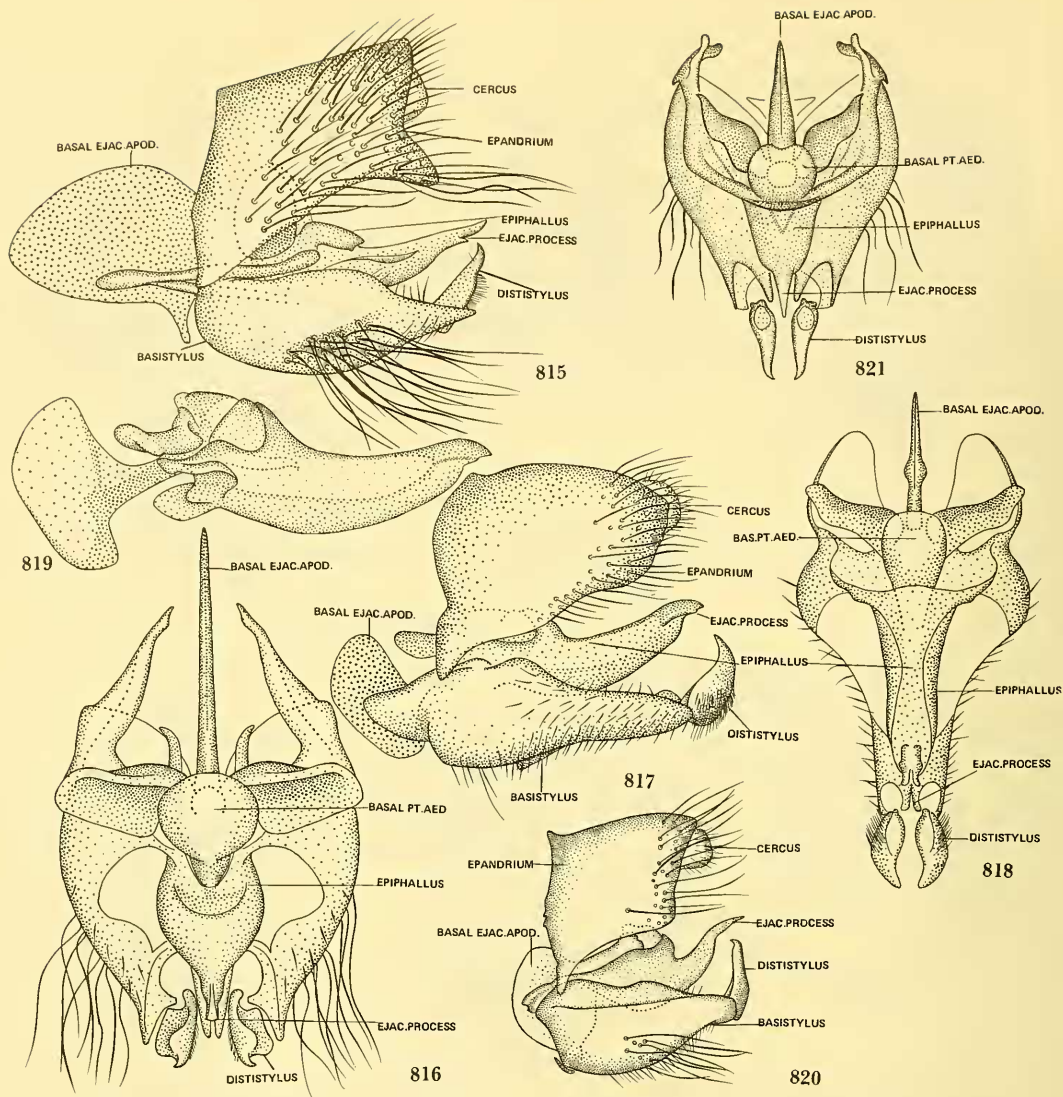
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bertaini Engel, lateral aspect. 804, *Paratoxophora cuthbertsoni* Engel, dorsal aspect. 805, *Sparnopolius lherminierii* Macquart, lateral aspect. 806, *Sparnopolius lherminierii* Macquart, dorsal aspect.



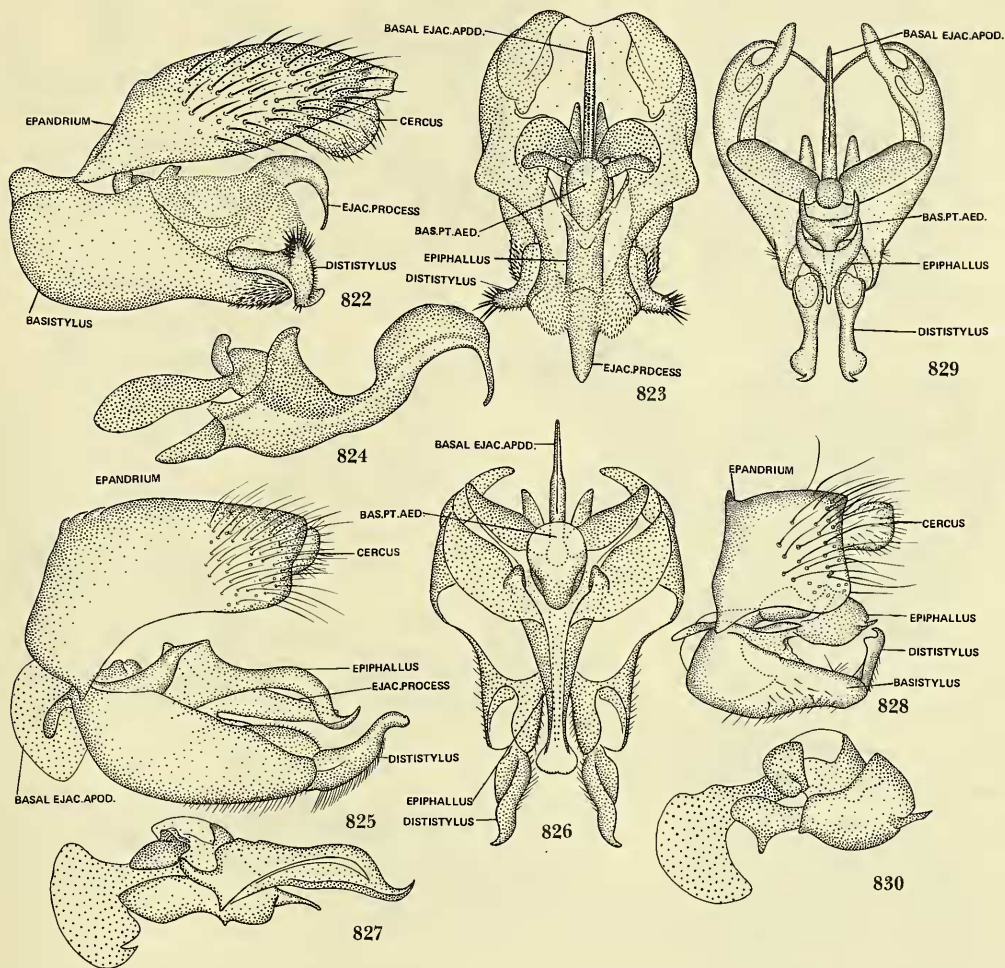
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Sosiomyia carnata Bezzi, dorsal aspect. 812, *Halidia plumipilosa* Hull, lateral aspect. 813, *Halidia plumipilosa* Hull, dorsal aspect. 814, *Halidia plumipilosa* Hull, axial system.



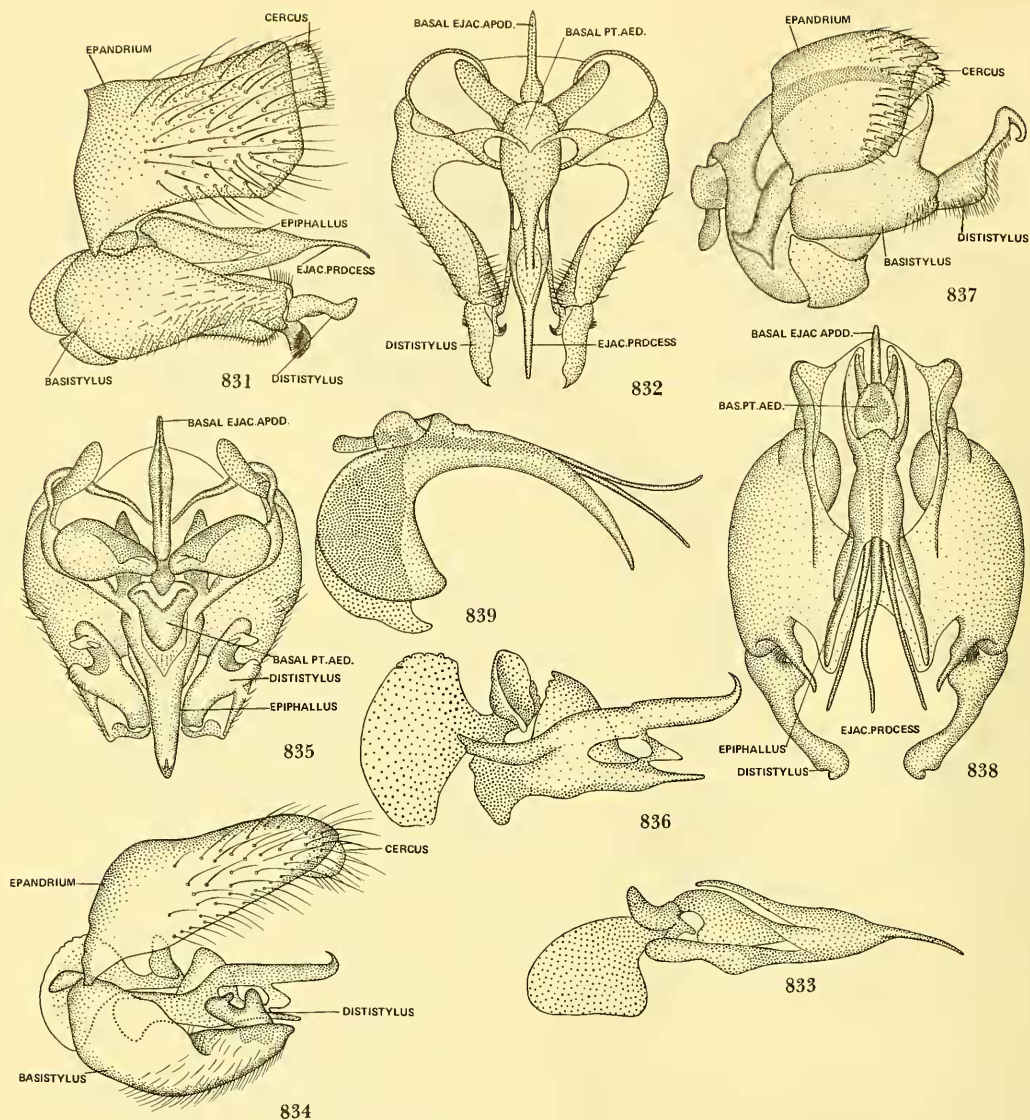
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mann, dorsal aspect. 819, *Corsomyza simplex* Wiedemann, axial system. 820, *Conophorus nigripennis* Loew, lateral aspect. 821, *Conophorus nigripennis* Loew, dorsal aspect.



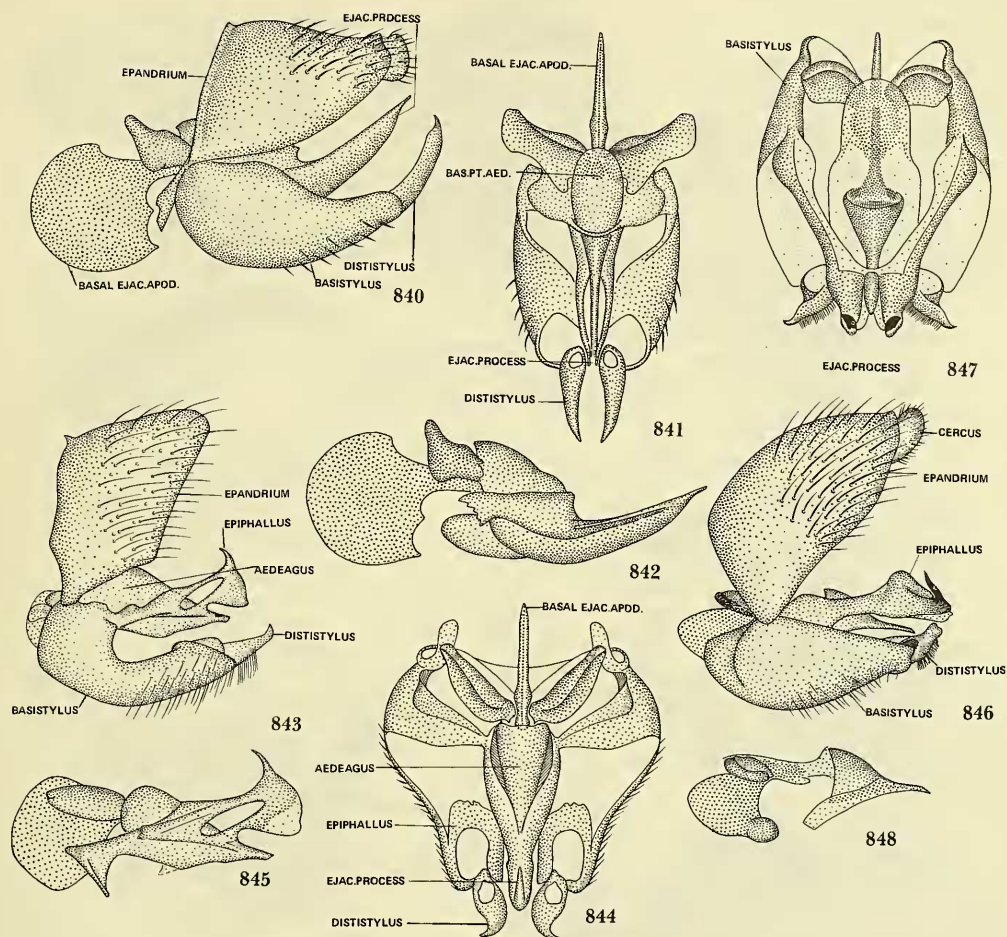
FIGURES 822-830.—822, *Oniromyia pachyceratus* Bigot, lateral aspect. 823, *Oniromyia pachyceratus* Bigot, dorsal aspect. 824, *Oniromyia pachyceratus* Bigot, axial system. 825, *Cytherea obscura* Fabricius, lateral aspect. 826, *Cytherea obscura* Fabri-

cus, dorsal aspect. 827, *Cytherea obscura* Fabricius, axial aspect. 828, *Pantarbes willistoni* Osten Sacken, lateral aspect. 829, *Pantarbes willistoni* Osten Sacken, dorsal aspect. 830, *Pantarbes willistoni* Osten Sacken, axial aspect.



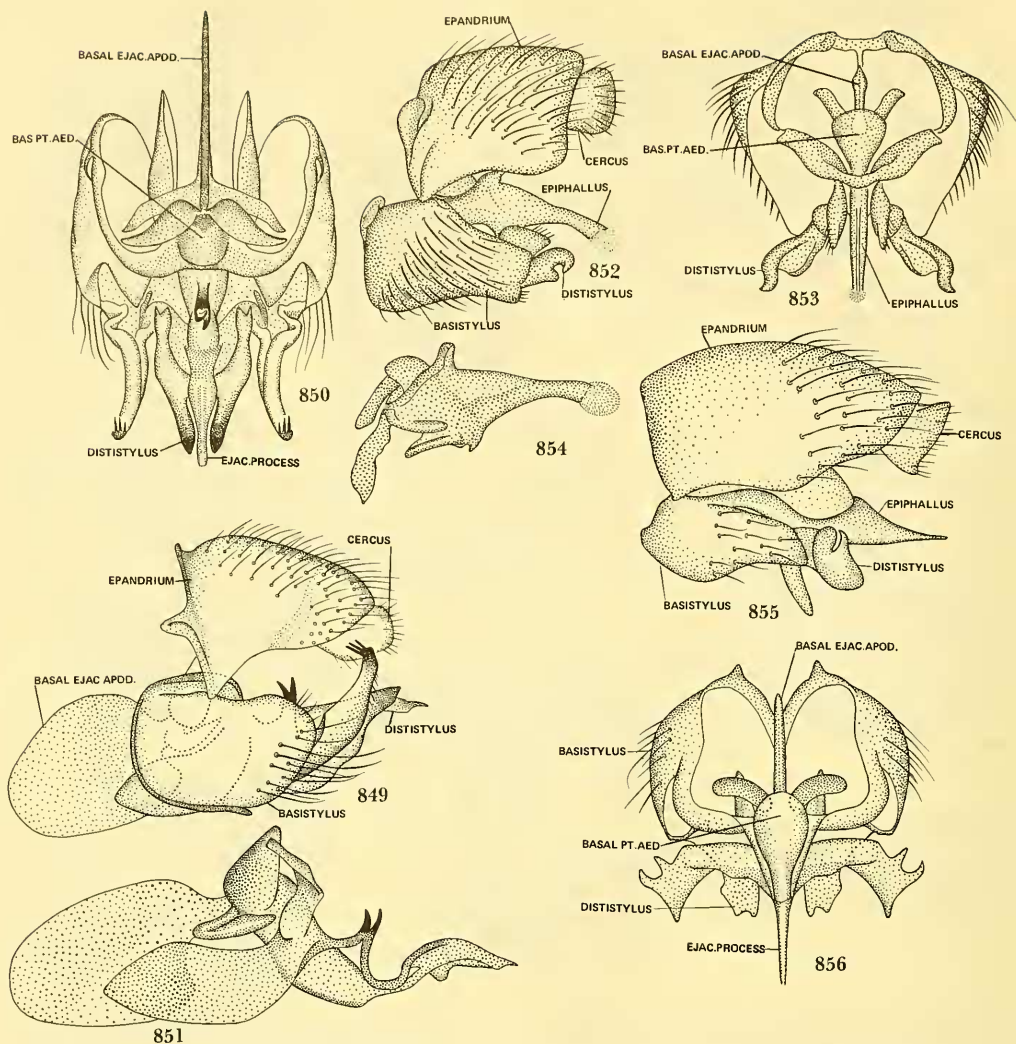
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robustum Osten Sacken, dorsal aspect. 836, *Heterostylum robustum* Osten Sacken, axial system. 837, *Heterotropus indicus* Nurse, lateral aspect. 838, *Heterotropus indicus* Nurse, dorsal aspect. 839, *Heterotropus indicus* Nurse, axial system.



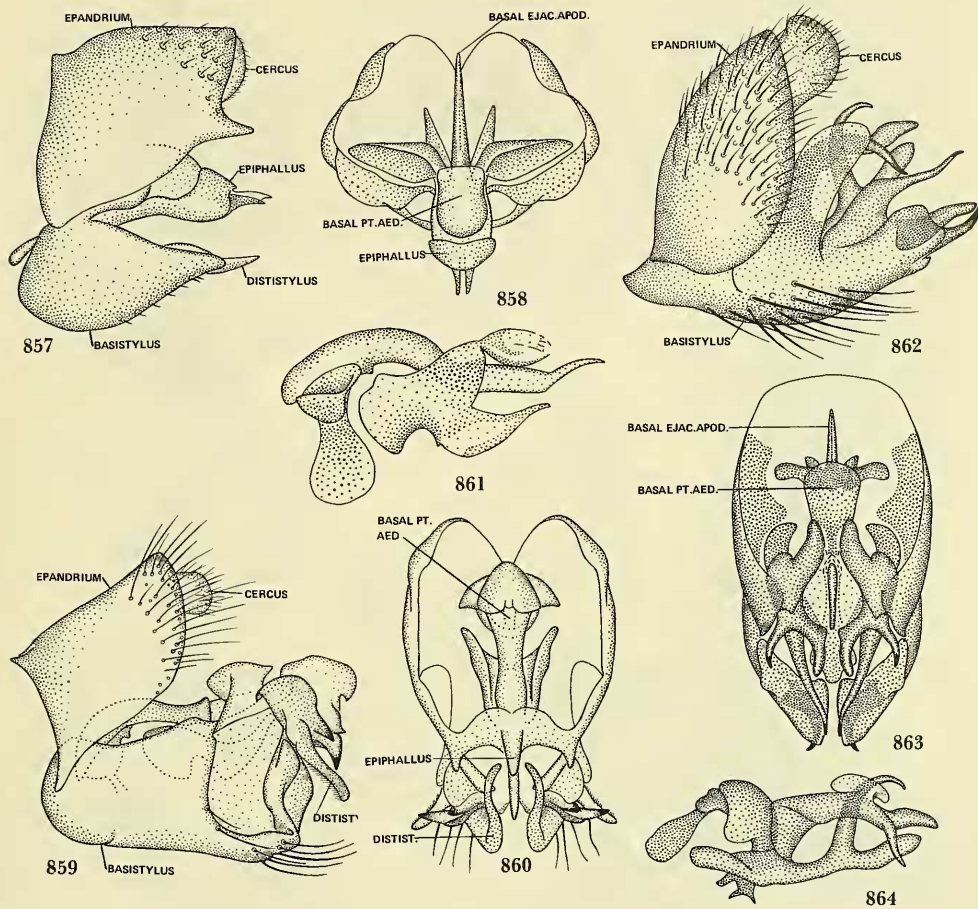
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Macquart, dorsal aspect. 845, *Triploecheus heteroneurus* Macquart, axial system. 846, *Desmatomyia anomala* Williston, lateral aspect. 847, *Desmatomyia anomala* Williston, dorsal aspect. 848, *Desmatomyia anomala* Williston, axial aspect.



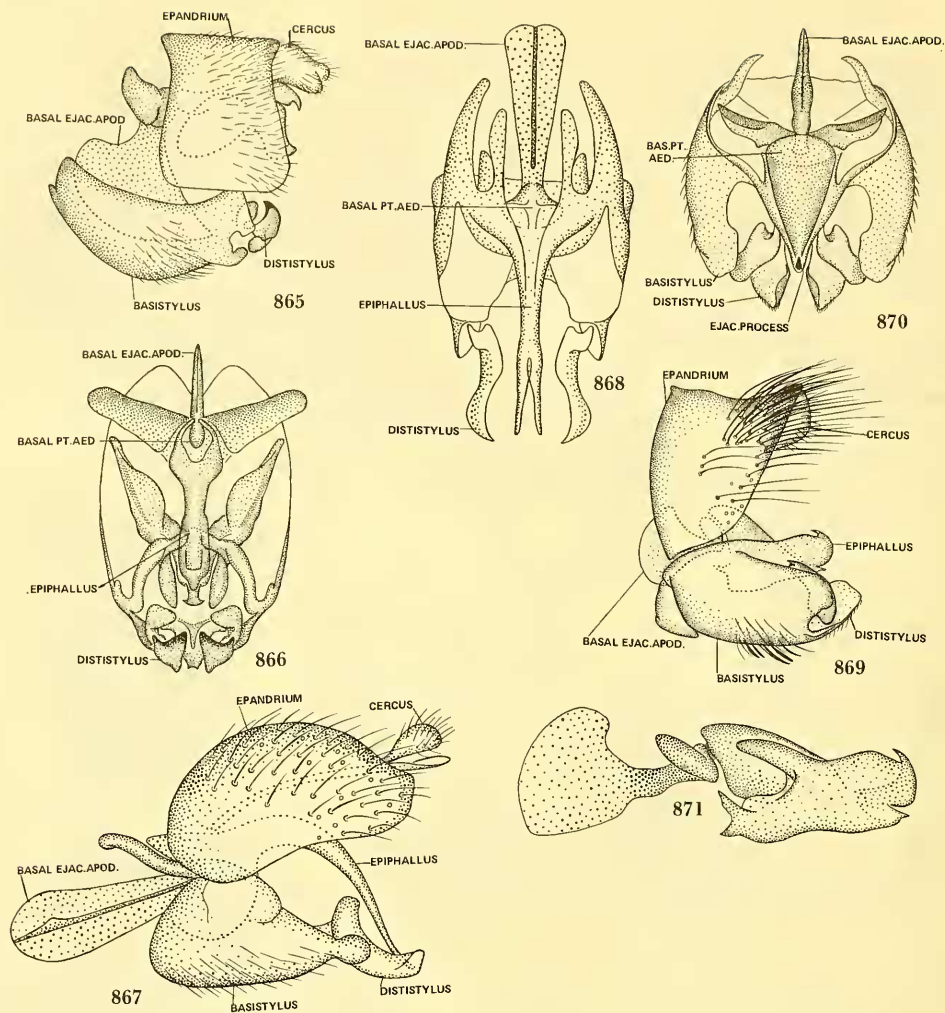
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854, *Usia (Parageron)* sp., axial system. 855, *Apolysis druas* Melander, lateral aspect. 856, *Apolysis druas* Melander, dorsal aspect.



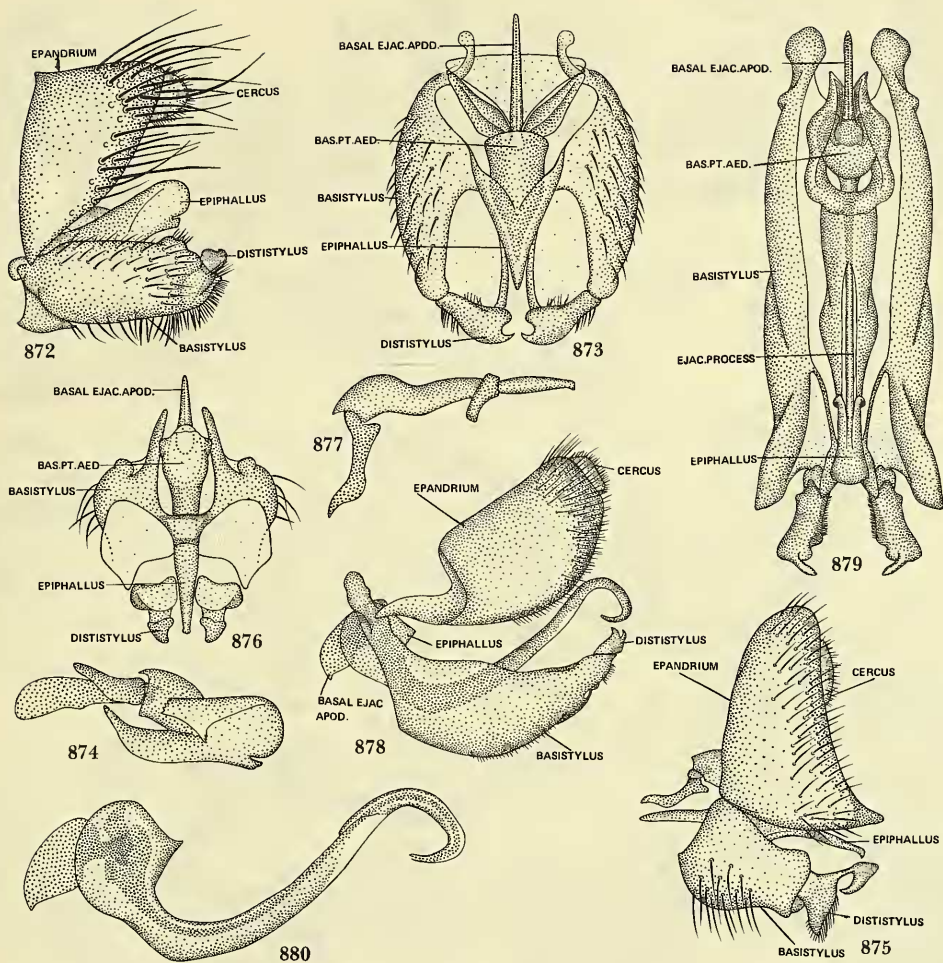
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Wiedemann, lateral aspect, 863, *Pseudoamictus heteropterus* Wiedemann, dorsal aspect. 864, *Pseudoamictus heteropterus* Wiedemann, axial system.



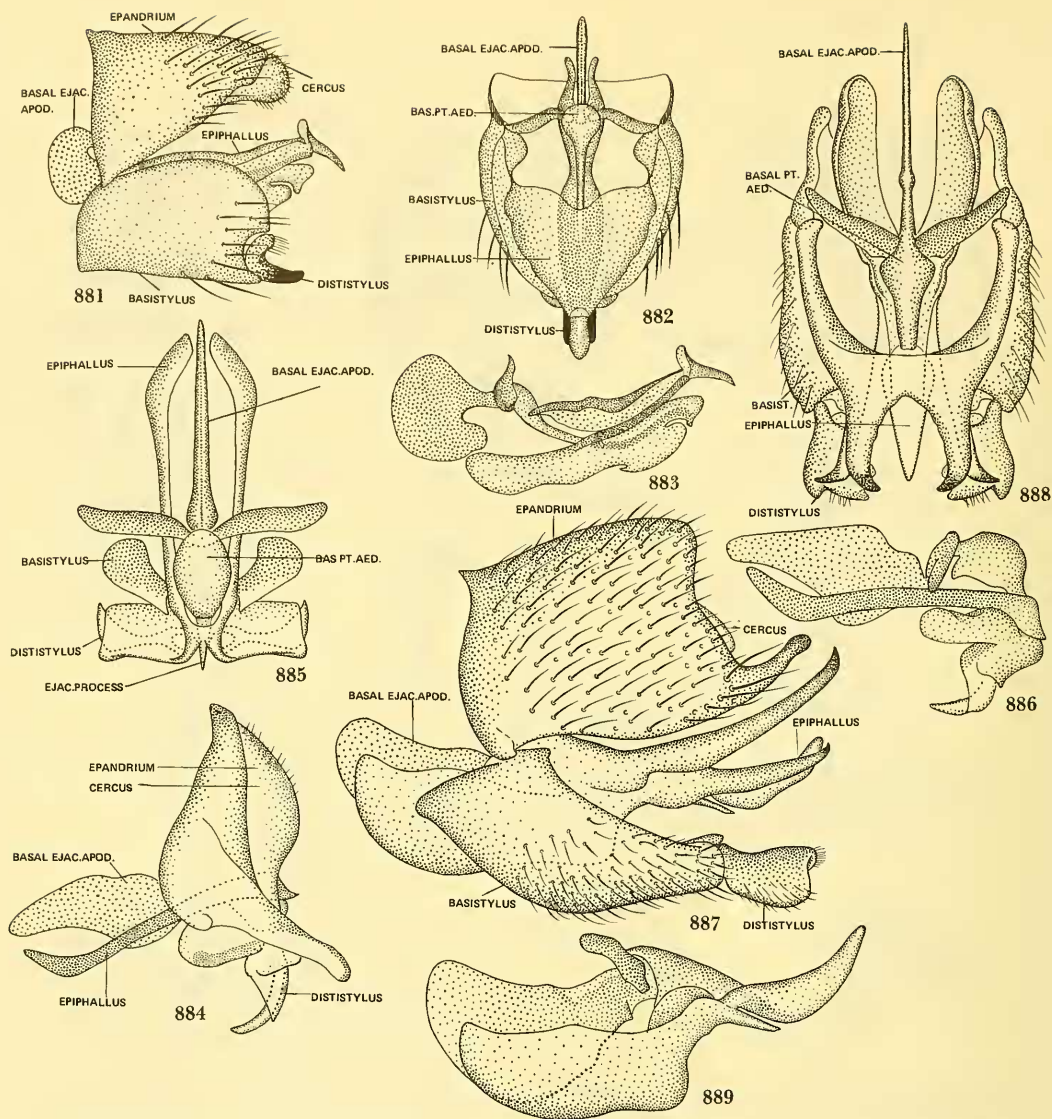
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dorsal aspect. 869, *Lepidophora lepidocera* Wiedemann, lateral aspect. 870, *Lepidophora lepidocera* Wiedemann, dorsal aspect. 871, *Lepidophora lepidocera* Wiedemann, axial system.



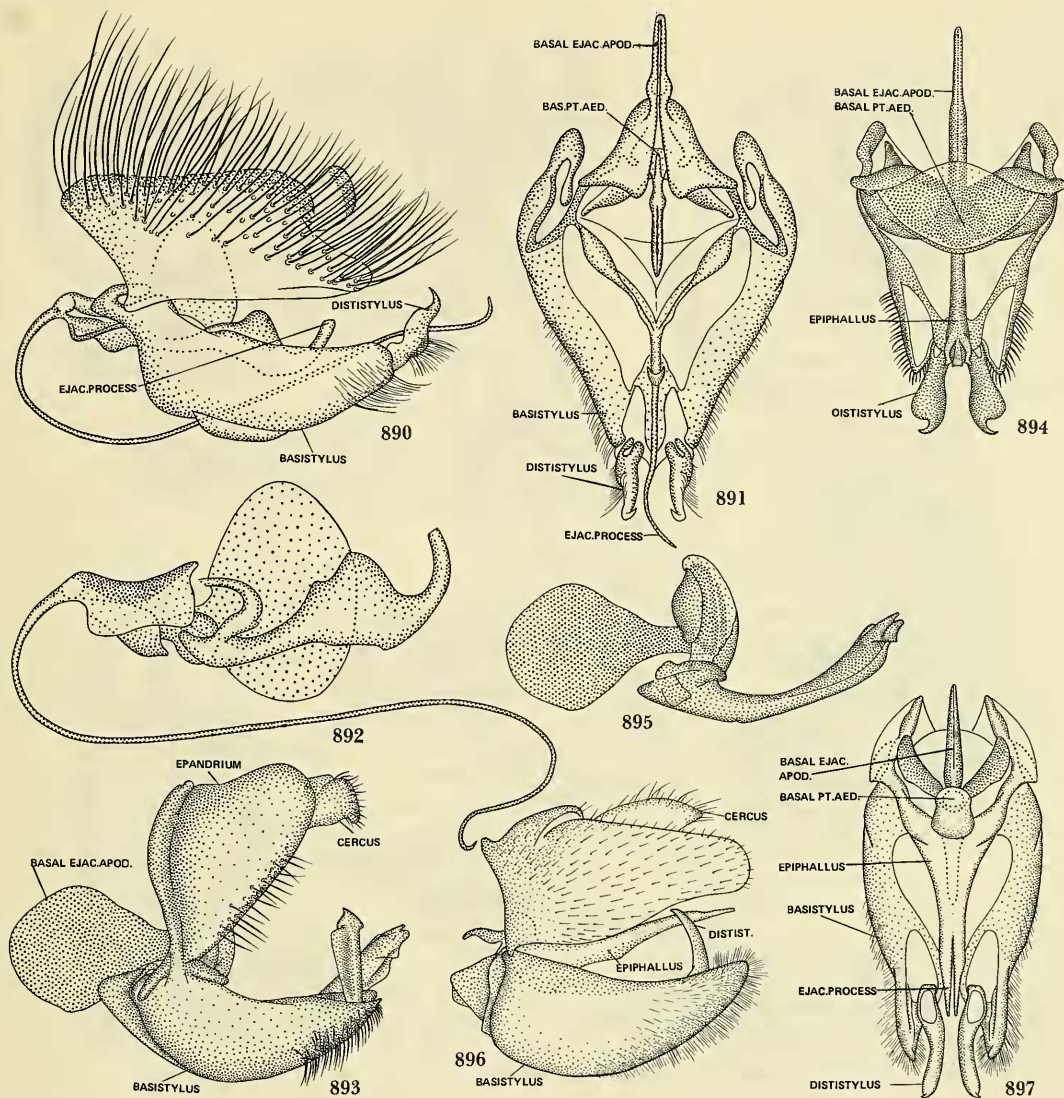
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paganica White, dorsal aspect. 877, *Cyrtomorpha paganica* White, axial system. 878, *Marmasoma sumptuosa* White, lateral aspect. 879, *Marmasoma sumptuosa* White, dorsal aspect. 880, *Marmasoma sumptuosa* White, axial system.



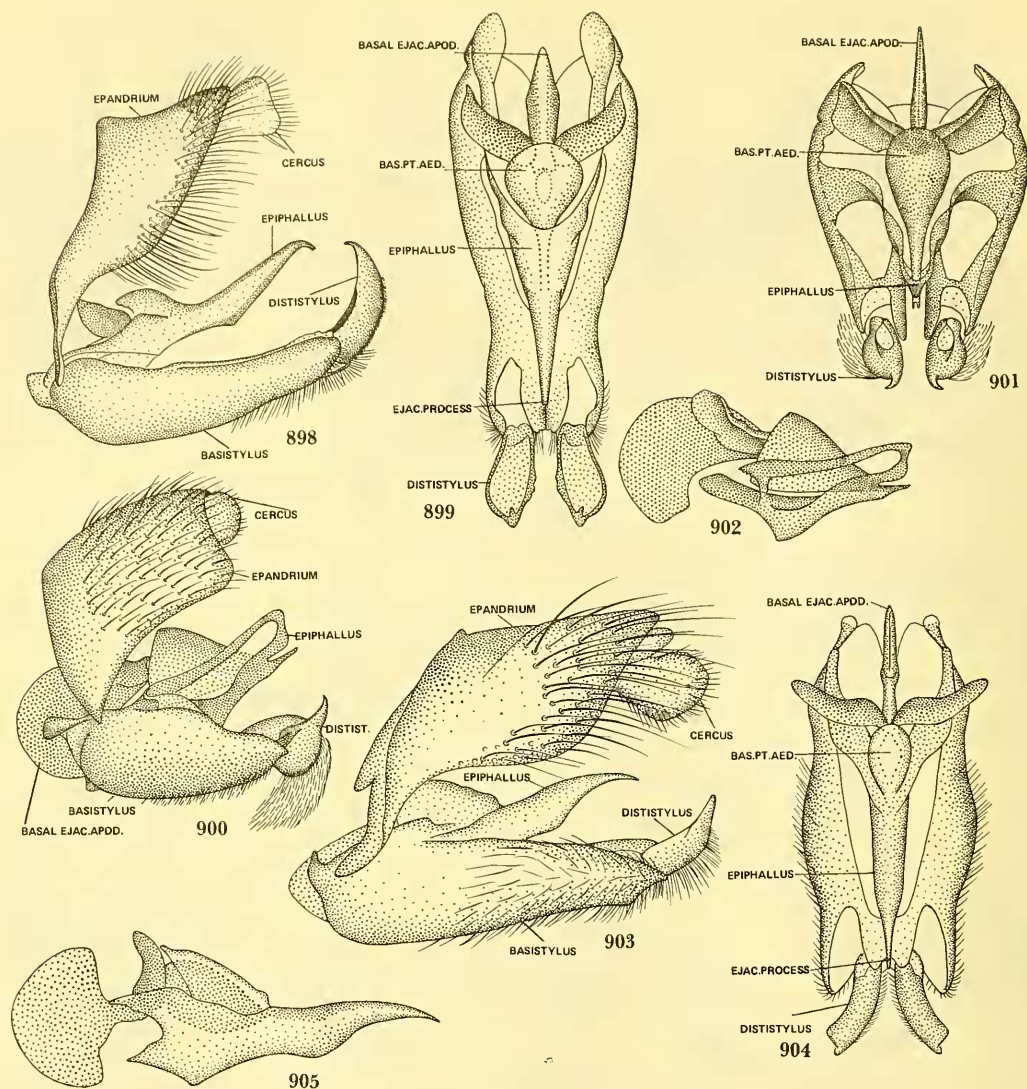
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monacha Melander, dorsal aspect. 886, *Mythicomomyia monacha* Melander, axial system. 887, *Systropus angulatus* Karsch, lateral system. 888, *Systropus angulatus* Karsch, dorsal system. 889, *Systropus angulatus* Karsch, axial system.



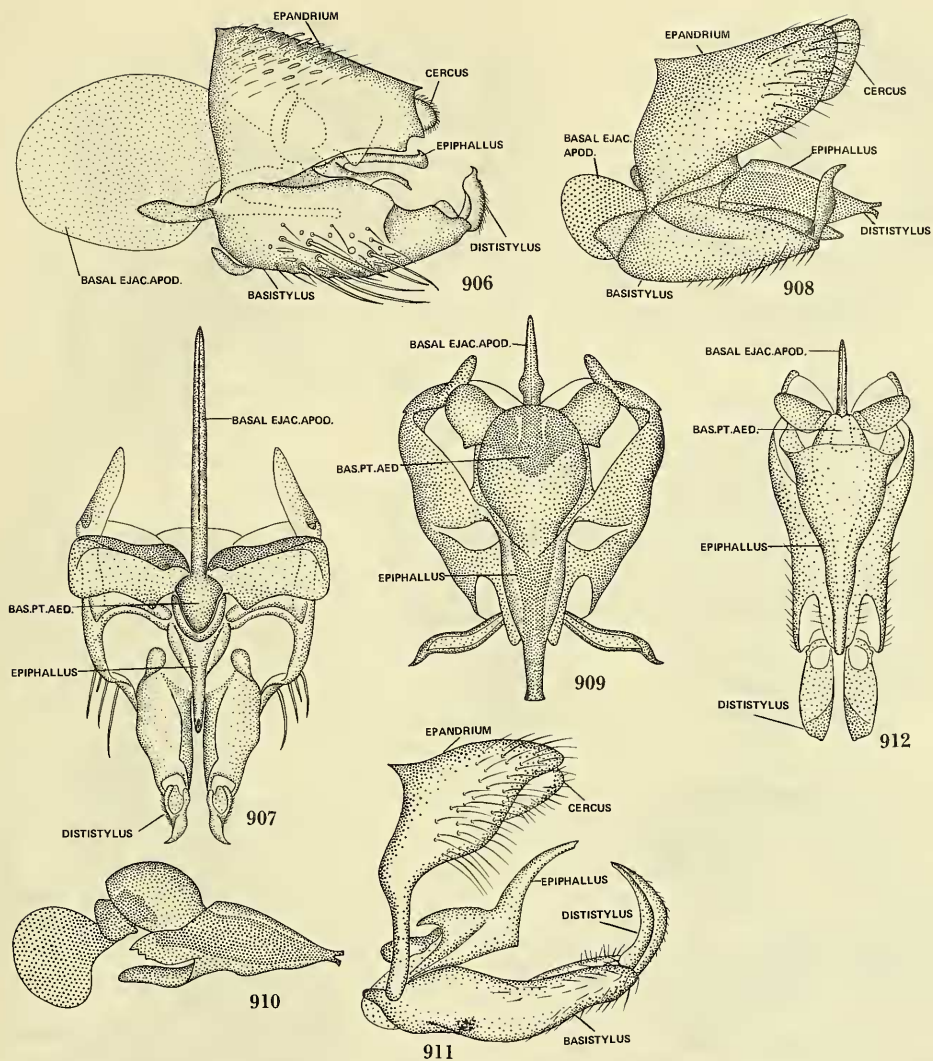
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895, *Peringueyimyia capensis* Bigot, axial system. 896, *Paracosmus morrisoni* Osten Sacken, lateral aspect. 897, *Paracosmus morrisoni* Osten Sacken, dorsal aspect.



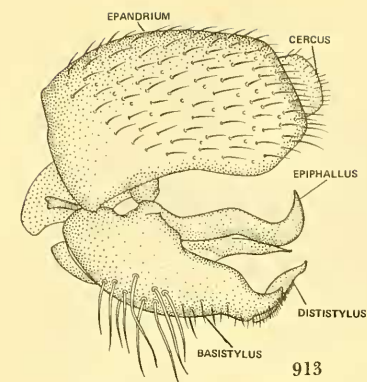
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Roberts, axial system. 903, *Lomatia sabaea* Fabricius, lateral aspect. 904, *Lomatia sabaea* Fabricius, dorsal aspect. 905, *Lomatia sabaea* Fabricius, axial system.

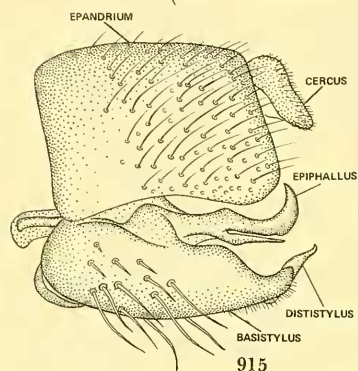


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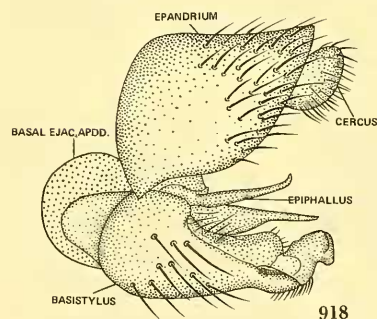
aspect. 910, *Desmatoneura argentifrons* Williston, axial system. 911, *Ogcodocera leucoprocta* Wiedemann, lateral aspect. 912, *Ogcodocera leucoprocta* Wiedemann, dorsal aspect.



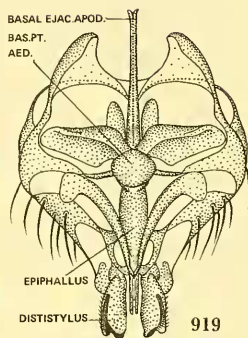
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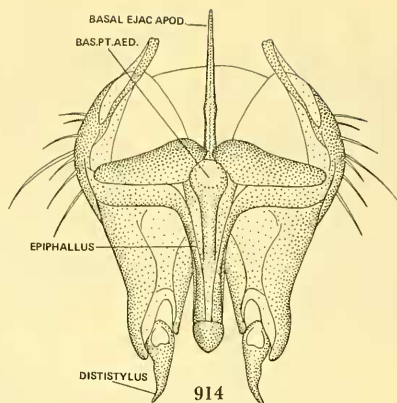
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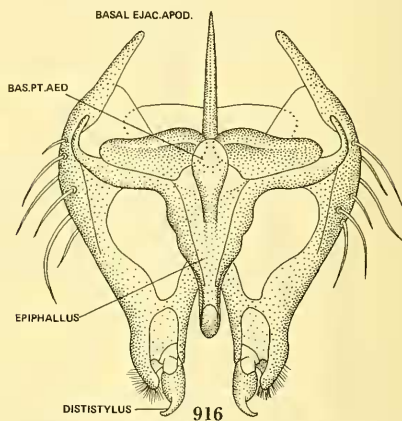
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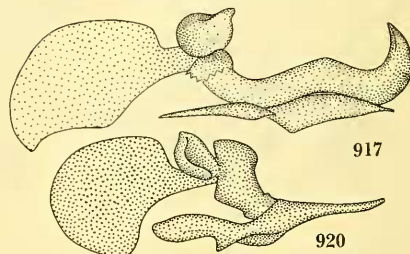
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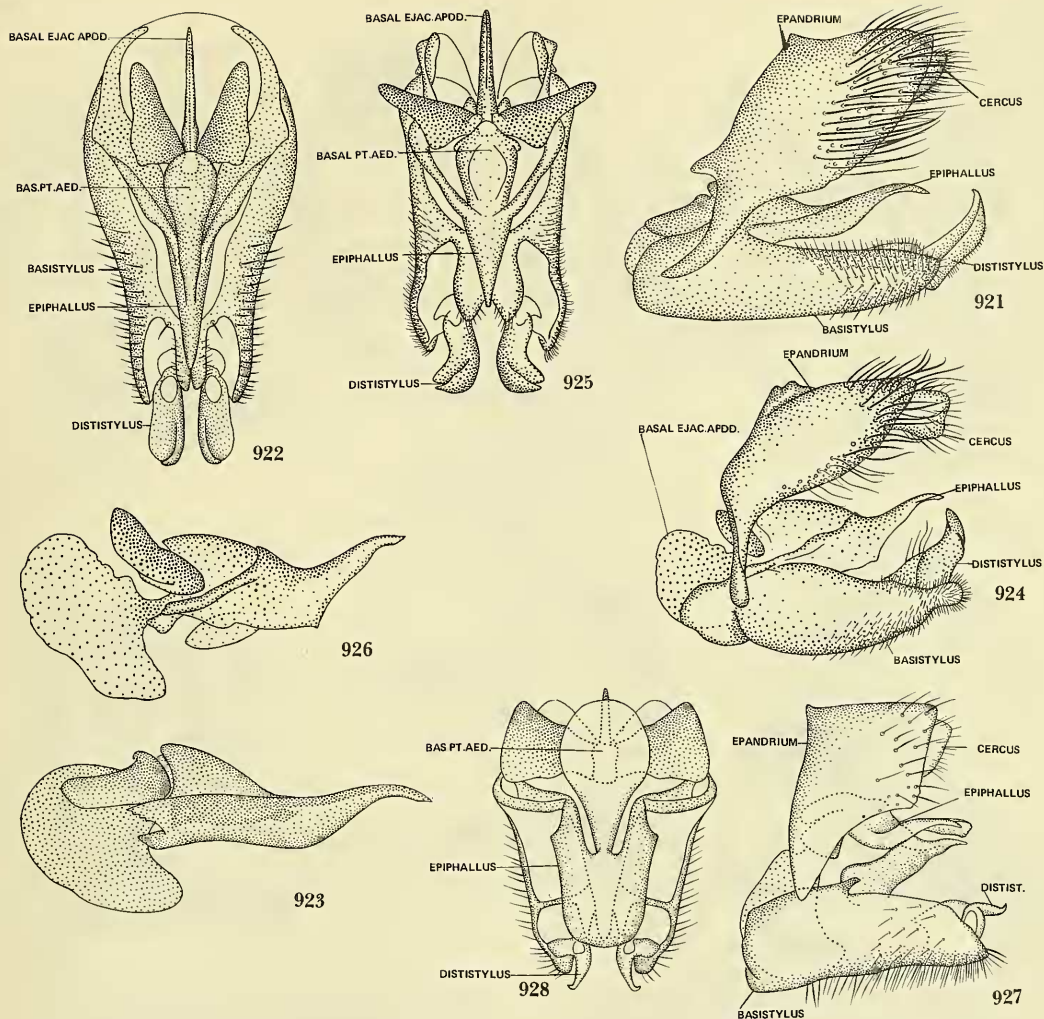


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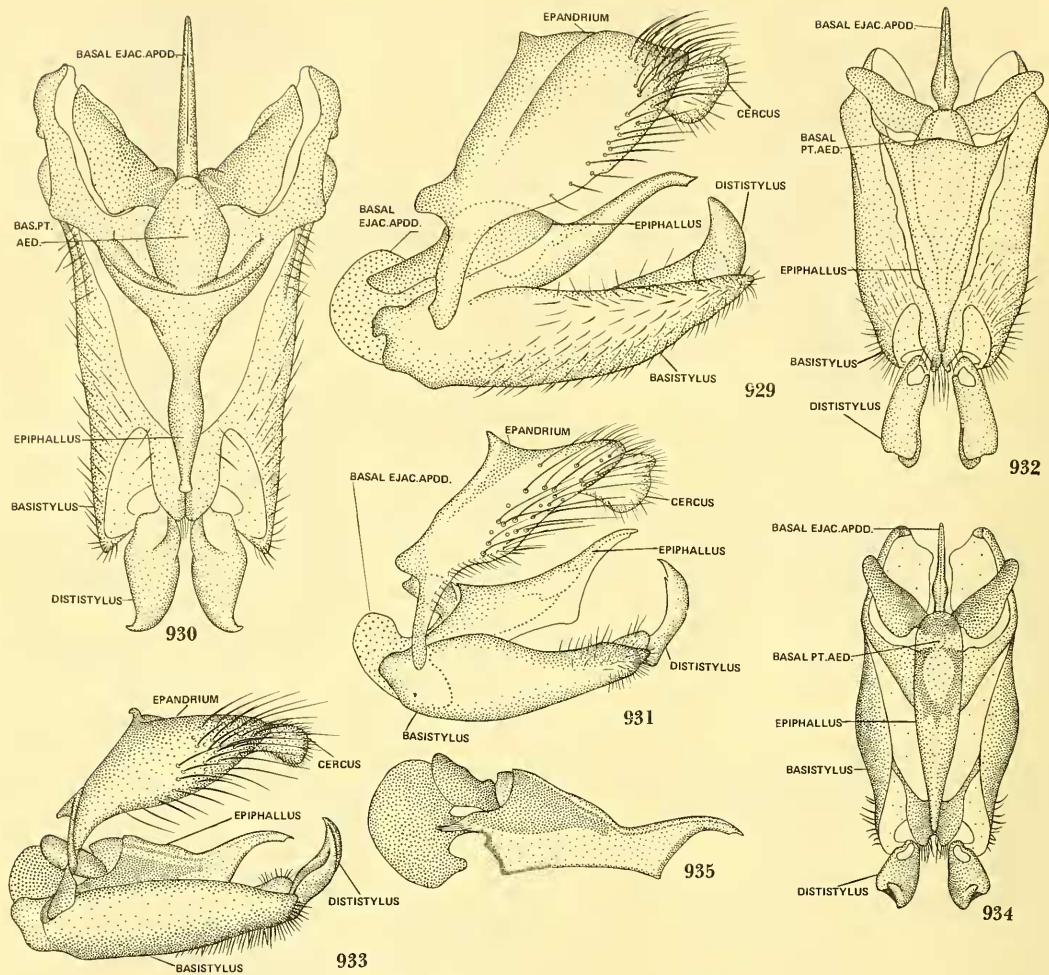
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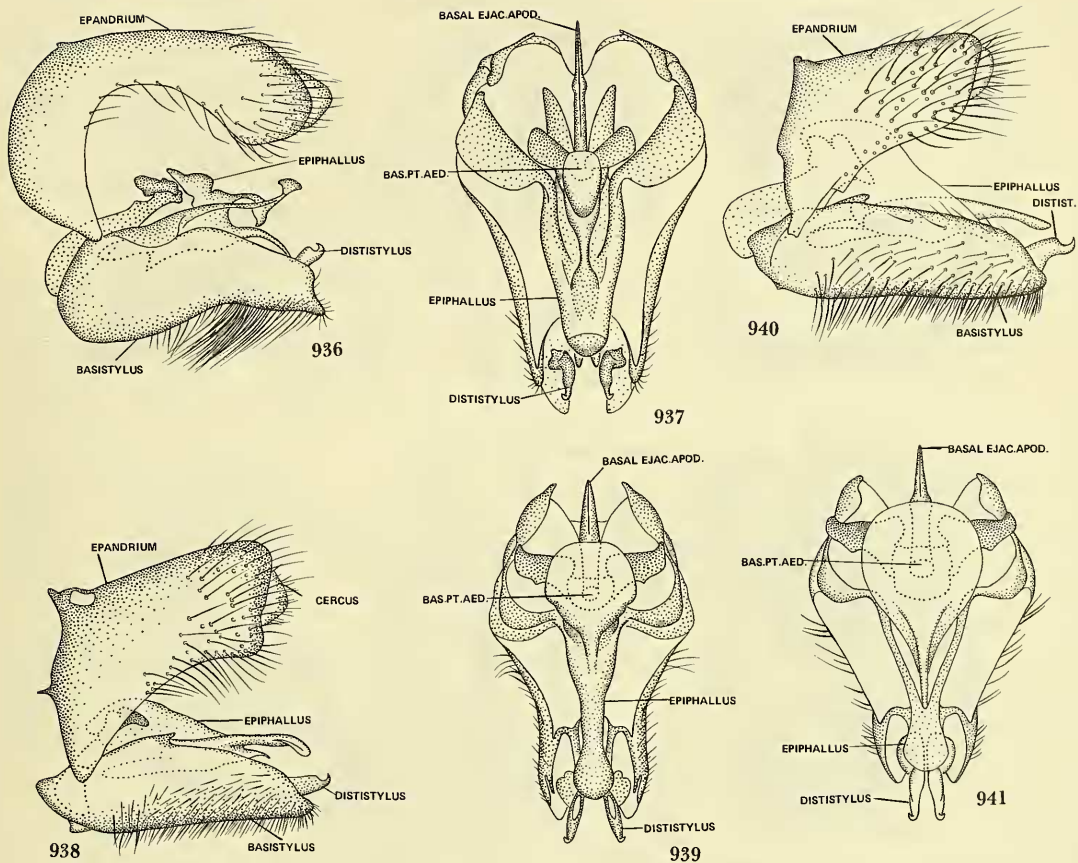
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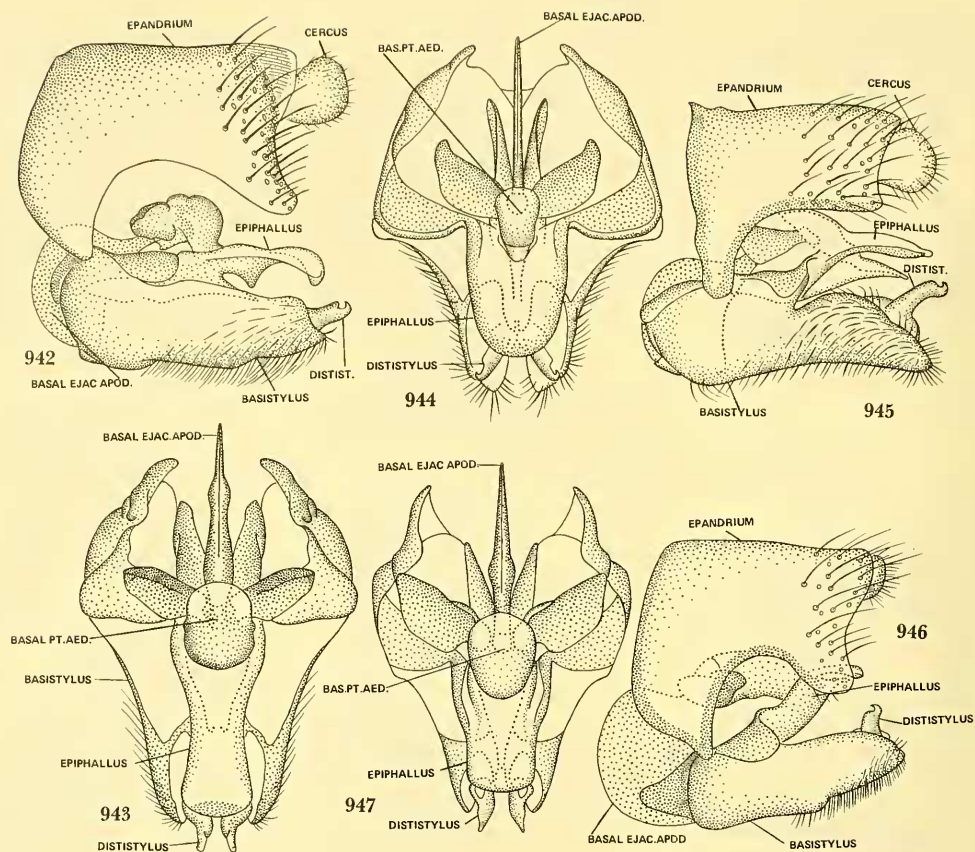
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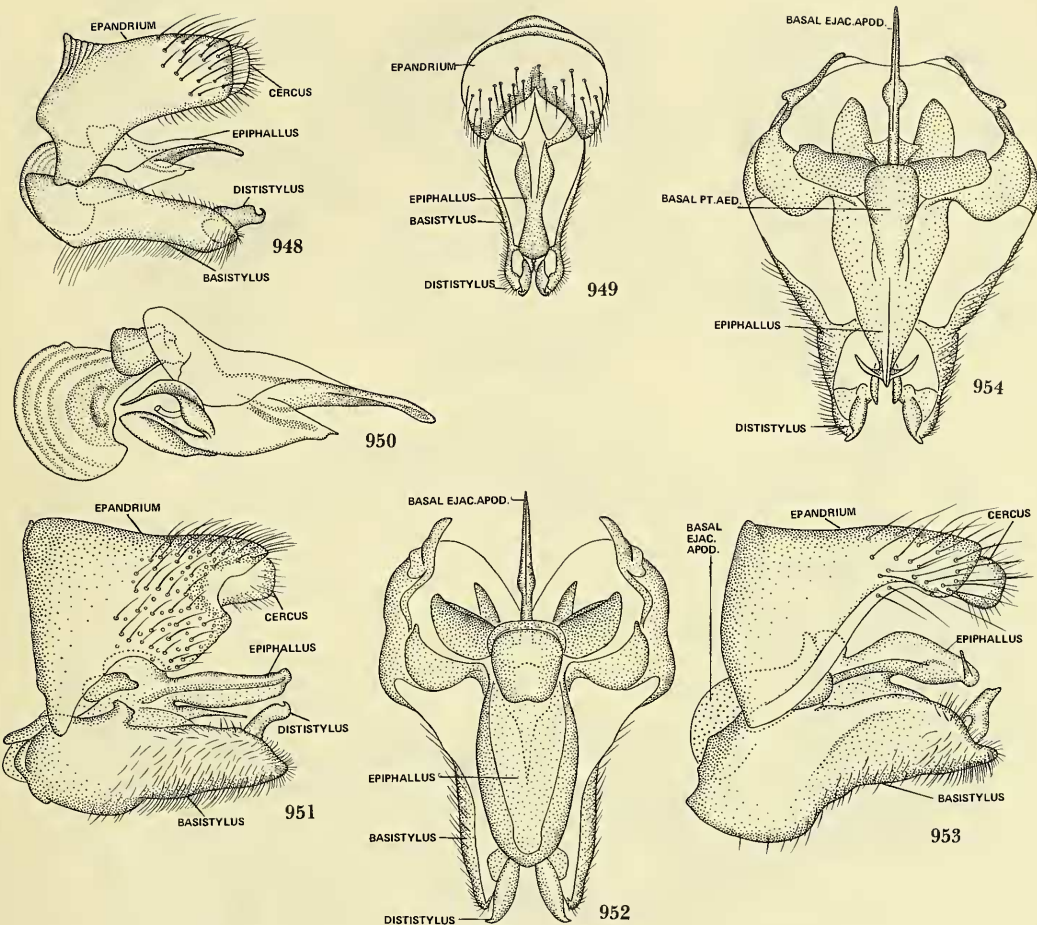
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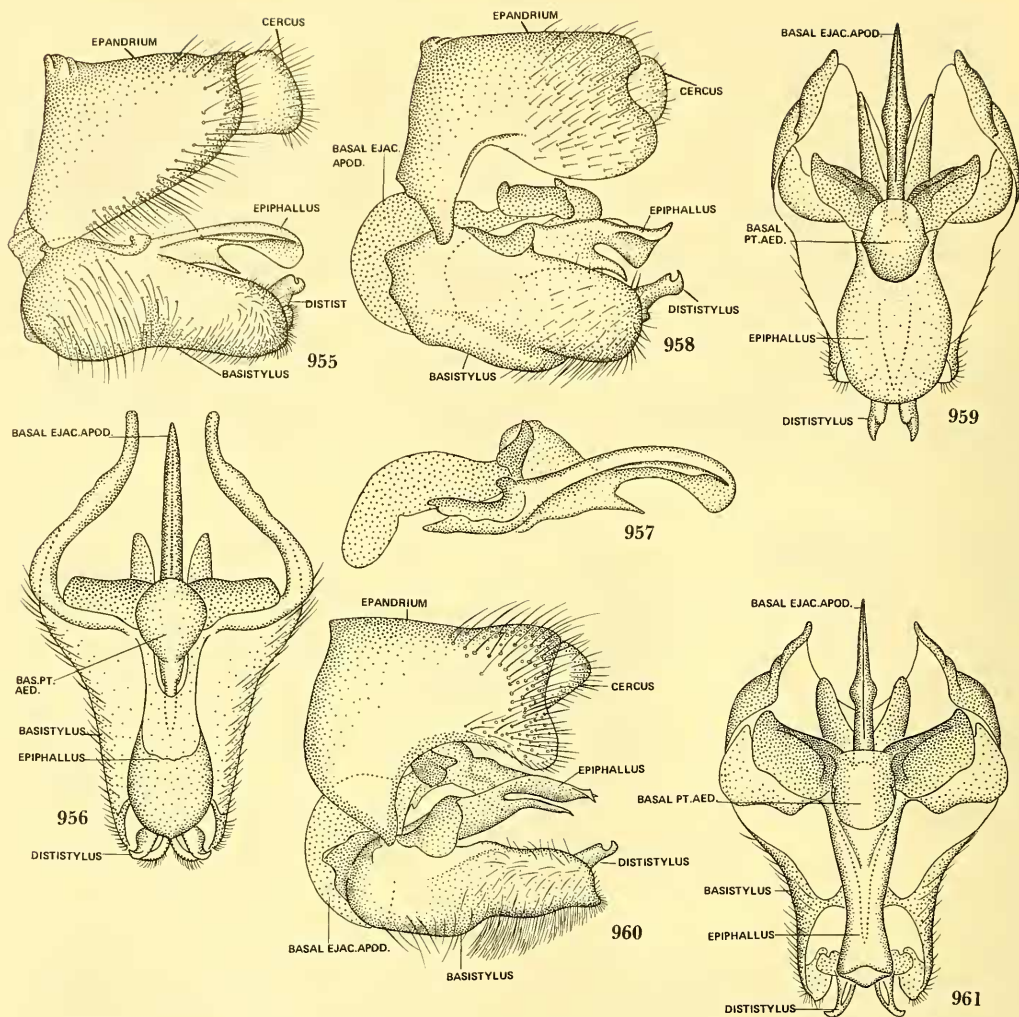
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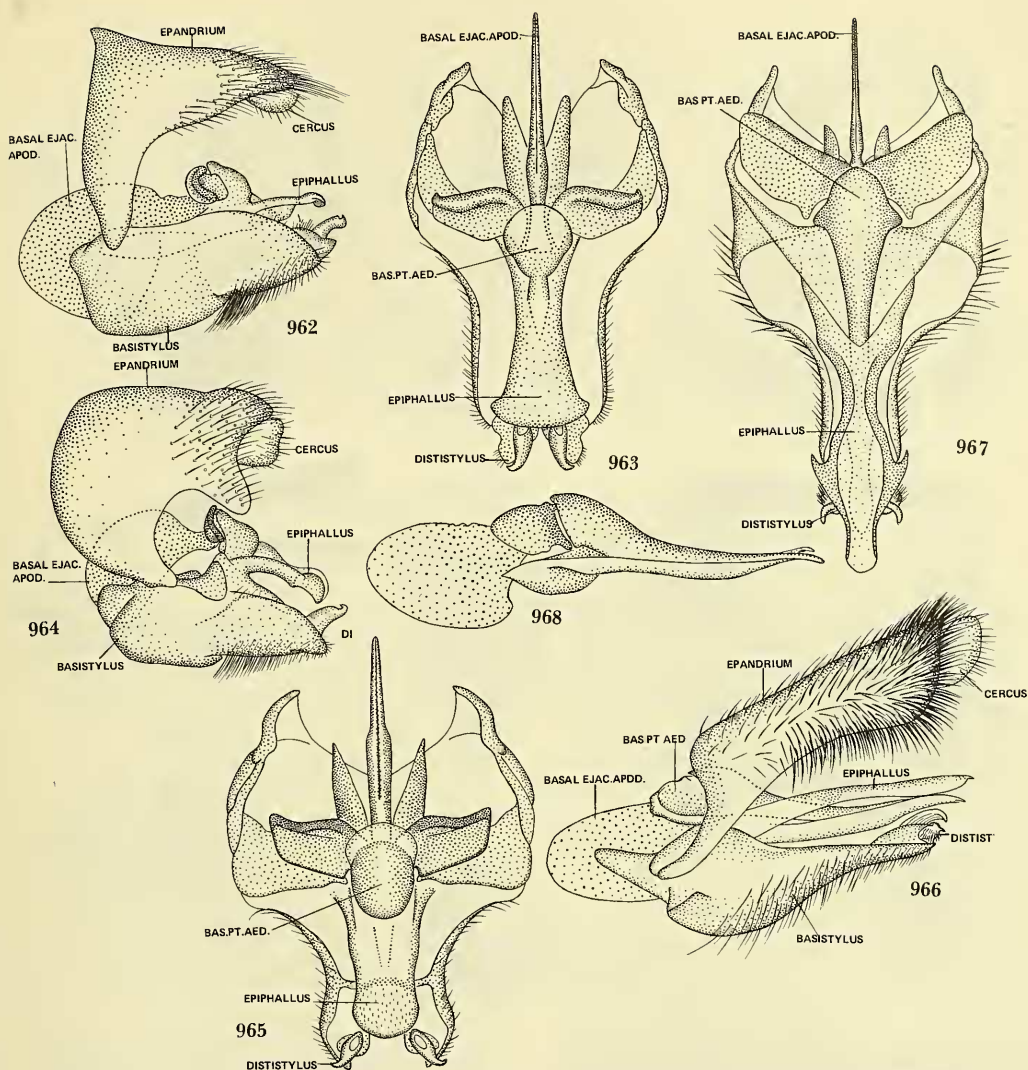
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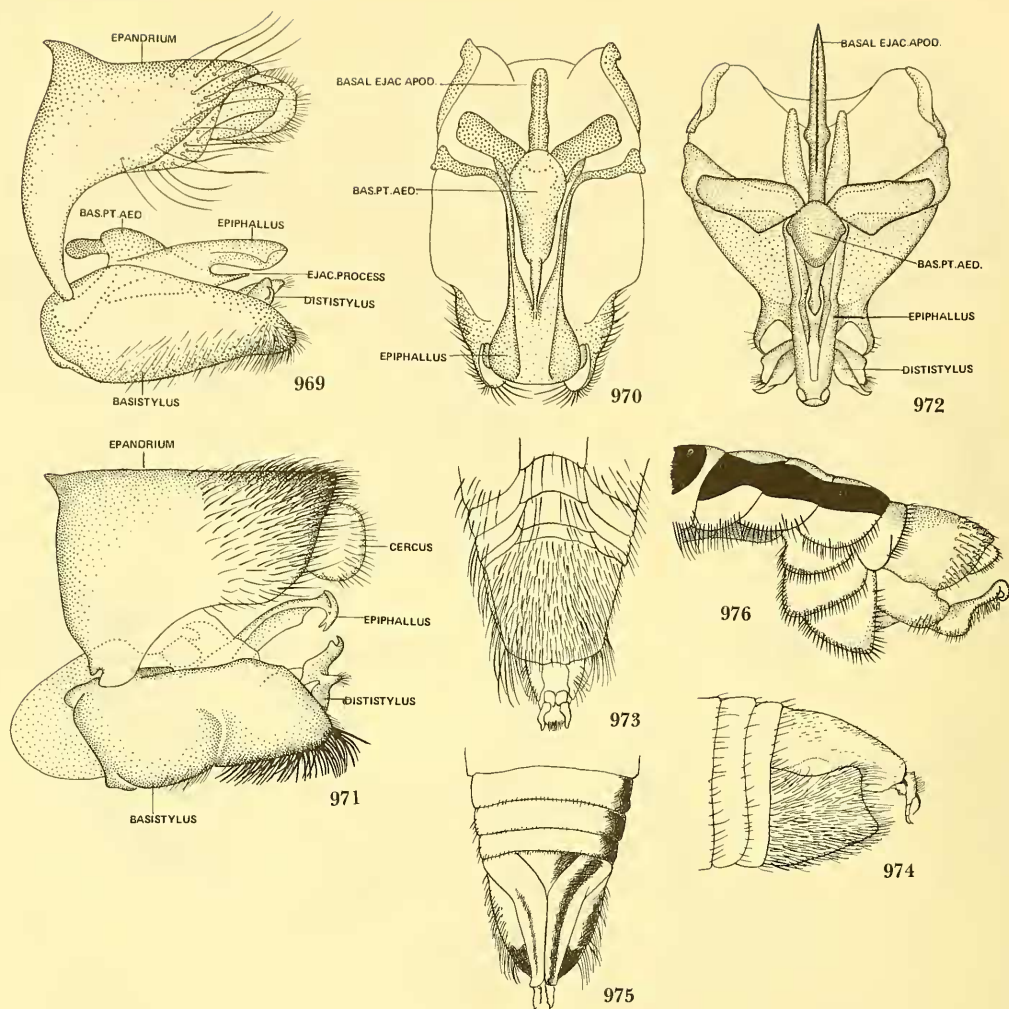
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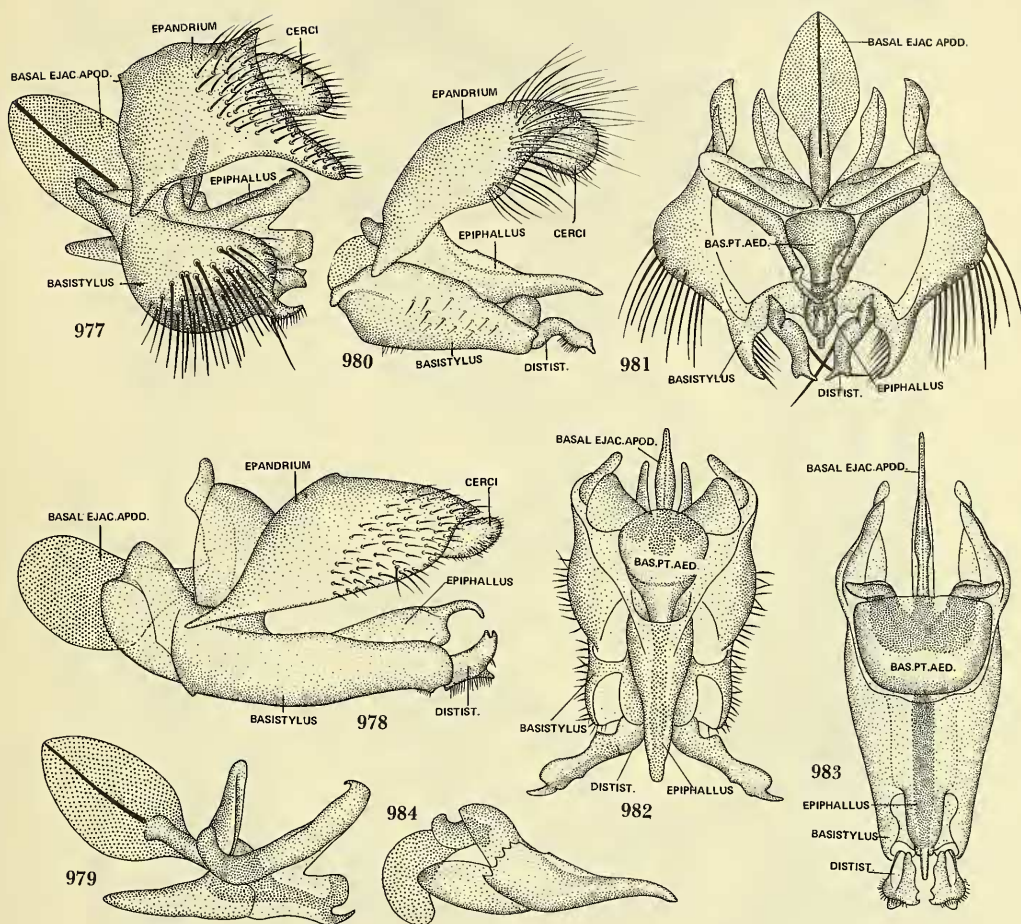
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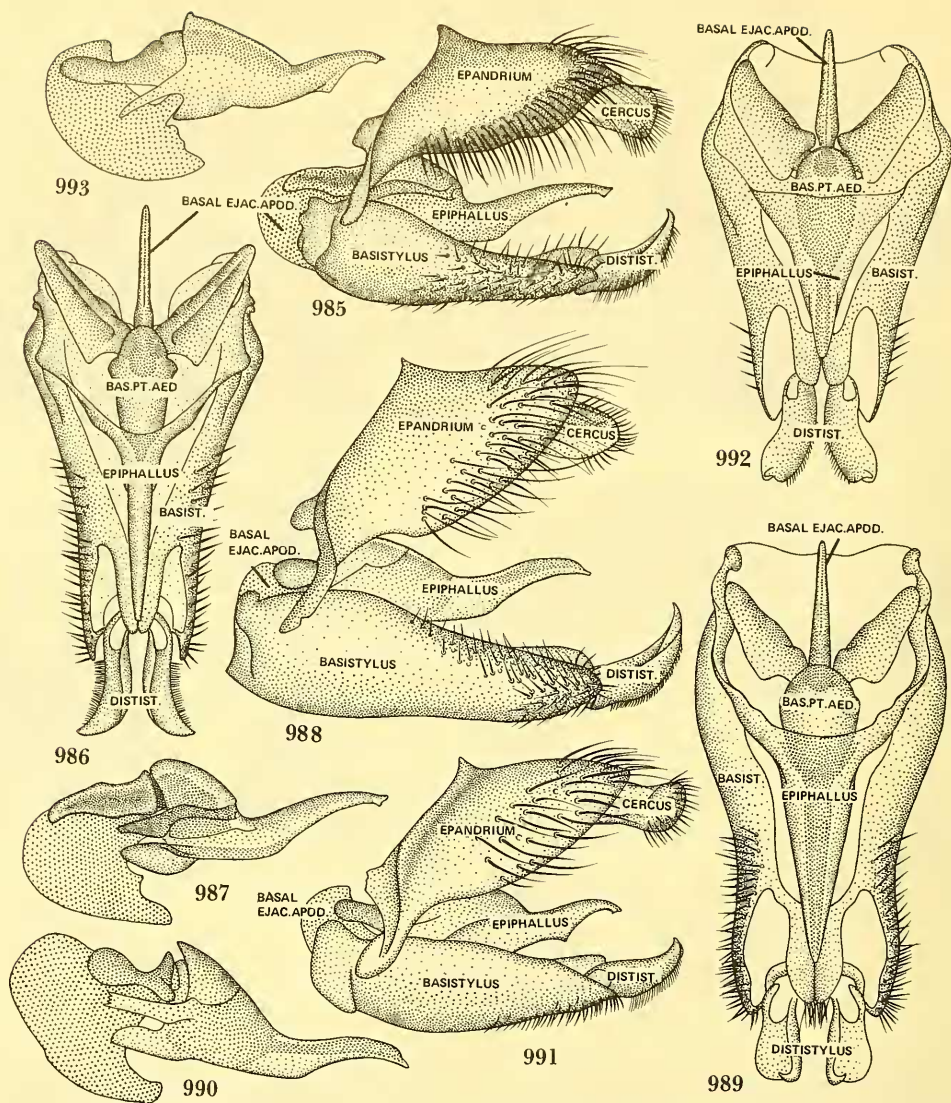
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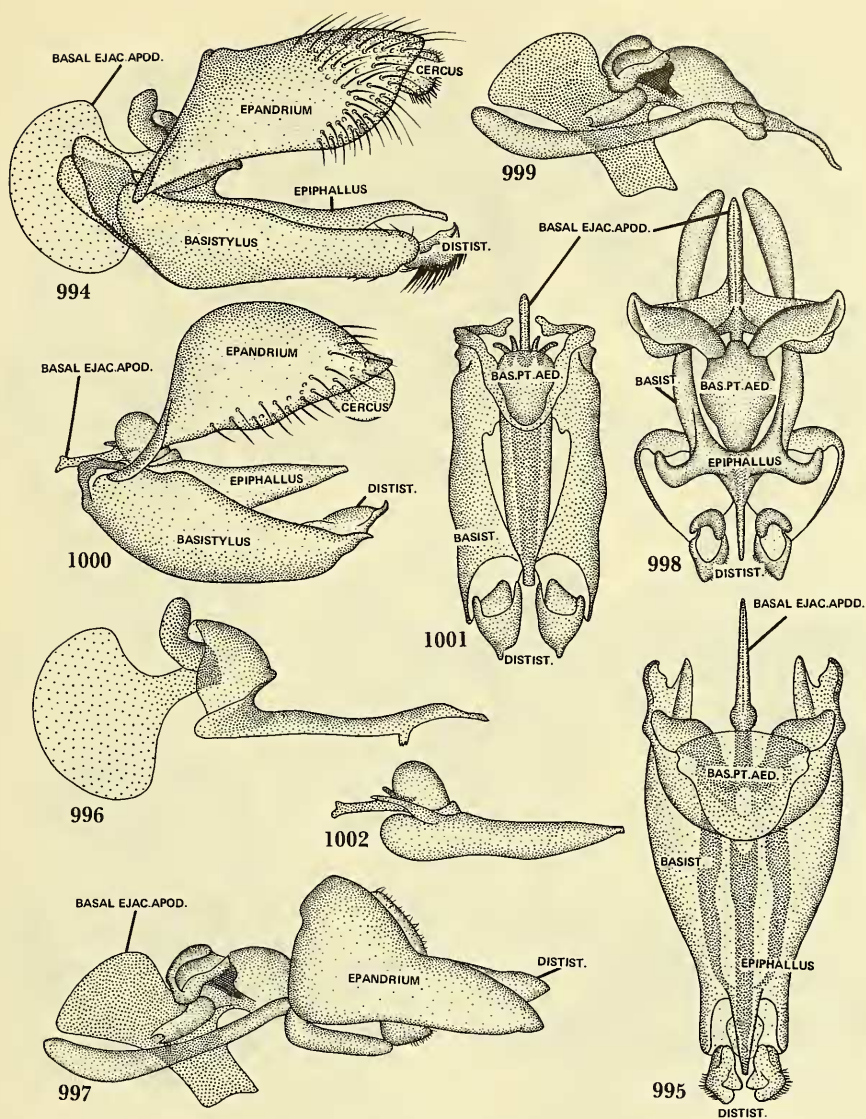
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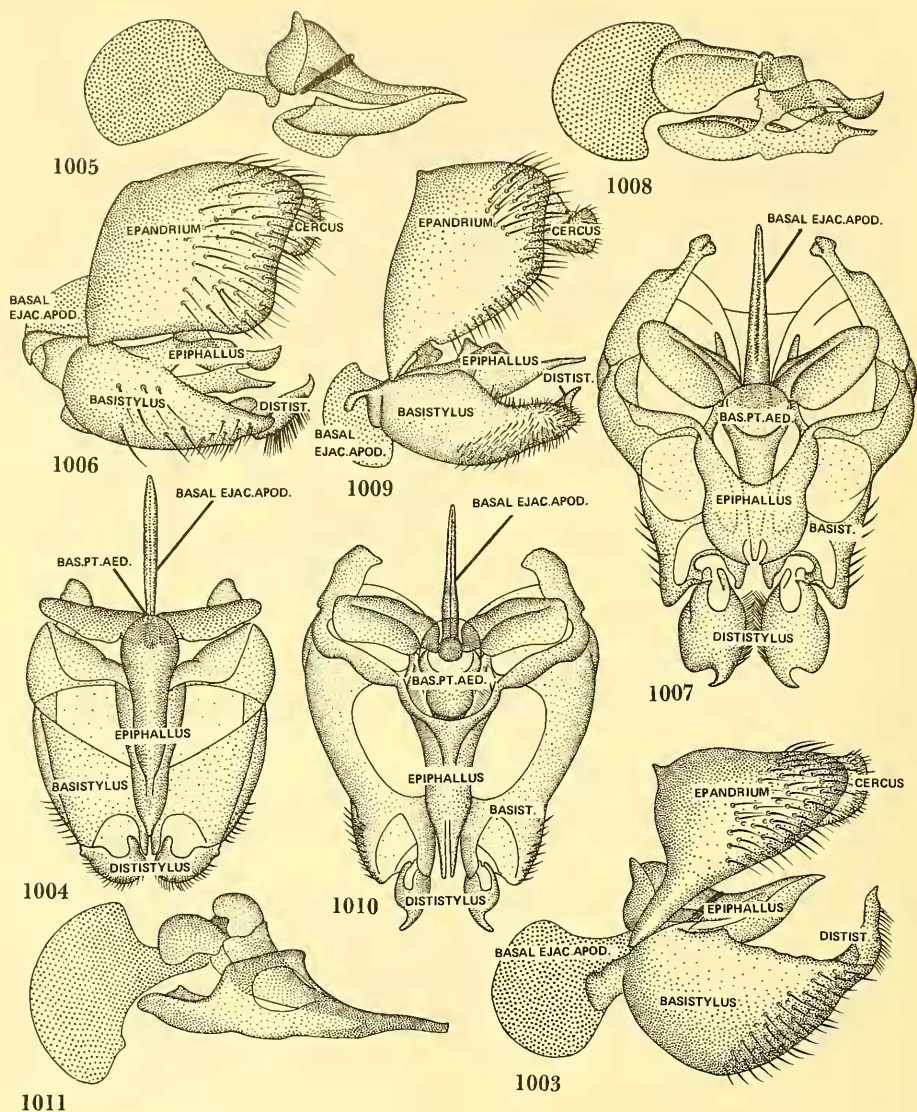
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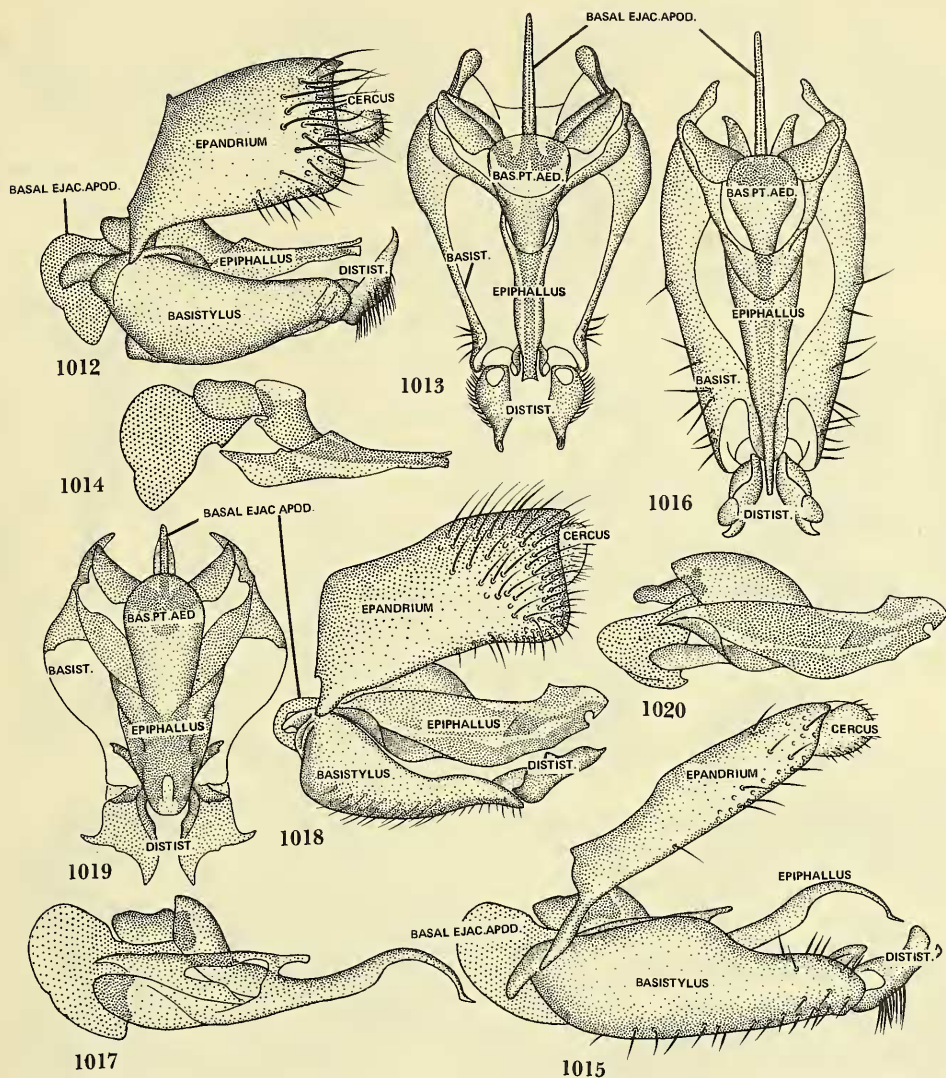
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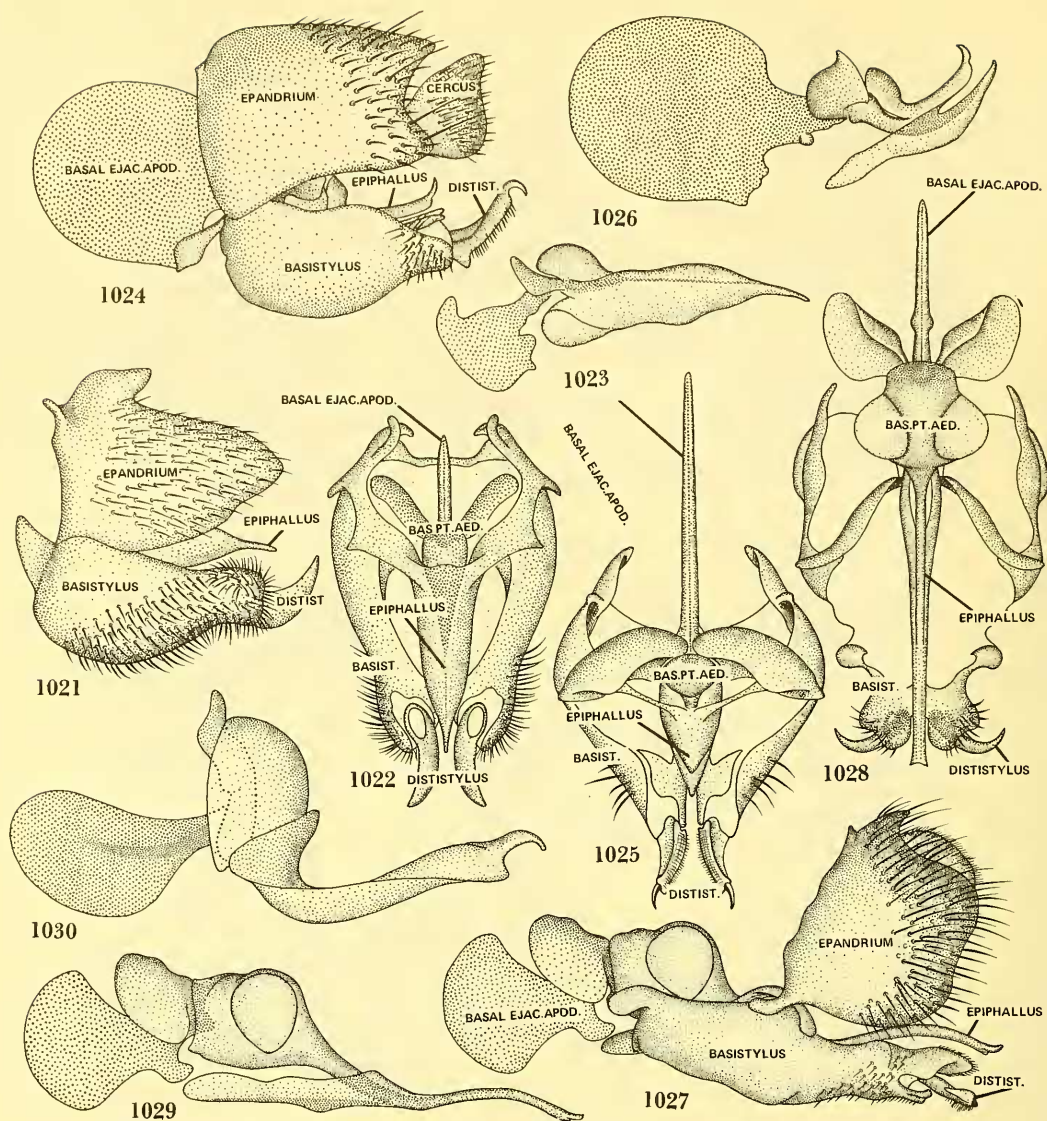
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